Wolfgang P. Dinter

Biogeography of the OSPAR Maritime Area

BfN
FEDERAL AGENCY FOR NATURE CONSERVATION

Biogeography of the OSPAR Maritime Area

A Synopsis and Synthesis of
Biogeographical Distribution Patterns
described for the North-East Atlantic

Wolfgang P. Dinter

Federal Agency for Nature Conservation
Bonn, Germany 2001

Figure on cover page: The OSPAR Maritime Area in an orthographical globe projection (W. P. Dinter)

Author, editing and cartography: Wolfgang P. Dinter
Federal Agency for Nature Conservation
Section for Marine and Coastal Nature Conservation
International Academy for Nature Conservation
Isle of Vilm
18581 Putbus, Germany

Scientific adviser at BfN: Dieter Boedeker

This publication is included to the literature database *„DNL-online“* (**www.DNL-online.de**).

Published by: Bundesamt für Naturschutz (BfN)
Federal Agency for Nature Conservation
Konstatinstr. 110, 53179 Bonn, Germany
Tel.: (+49) 228/8491-0, Fax: (+49) 228/8491-200
internet: http://www.bfn.de

Printed by: LV Druck im Landwirtschaftsverlag GmbH, Münster-Hiltrup

Orders: BfN-Schriftenvertrieb im Landwirtschaftsverlag
48084 Münster, Germany
Tel.: (+49) 2501/801-300, Fax: (+49) 2501/801-351
or internet: www.lv-h.de/bfn
Price: 12 €

ISBN: 3-7843-3818-6

Printed on acid-free paper

Bonn, Germany 2001

Contents

List of Acronyms and Abbreviations

AWI	Alfred Wegener Institute for Polar and Marine Research
AZT	Archibenthal Zone of Transition
BBL	Benthic Boundary Layer
BfN	(German) Federal Agency for Nature Conservation
b.p.	before present
BSPA	Baltic Sea Protected Area (HELCOM)
CBD	Convention on Biological Diversity (Rio de Janeiro 1992)
CCD	Carbonate Compensation Depth
CNPPA	Commission on National Parks and Protected Areas (of IUCN)
EEZ	Exclusive Economic Zone
e.g.	example given
EU	European Union
EU HD	EU Habitat Directive
EUNIS	European Nature Information System
ERMS	European Register of Marine Species (of the EU Marine Science and Technology Programme, MAST)
GBRMPA	Great Barrier Reef Marine Park Authority
GEBCO	General Bathymetric Charts of the Oceans (of the IOC)
GIS	Geographic Information System
GPS	Global Positioning System
GRIDÅ	Global Resource Information Database Årendal/Norway
GSDW	Greenland Sea Deep Water
HELCOM	Helsinki Commission – Baltic Marine Environment Protection Commission
HTV	Hydrothermal Vent
i.a.	inter alia
ICES	International Council for the Exploration of the Sea
IEO	Instituto Español de Oceanografía
IFREMER	Institut français de recherche pour l'exploitation de la mer
IOC	Intergovernmental Oceanographic Commission
IMO	International Maritime Organisation
ISA	International Seabed Authority (of UNCLOS)
IUCN	The World Conservation Union (formerly: International Union for the Conservation of Nature and Natural Resources)
JNCC	Joint Nature Conservation Comitee (U.K.)
LME	Large Marine Ecosystem
MAB	Man And Biosphere Program (of the UNESCO)
MAP	Madeira Abyssal Plain
MAR	Mid-Atlantic Ridge
MNCR	Marine Nature Conservation Review (of the JNCC)
MPA	Marine Protected Area

NAD	North Atlantic Drift
NADW	North Atlantic Deep Water
NATURA	Habitat Directive of the EU
N.COUNC	Nordic Council of Ministers: MPAs in the nordic countries
NEA	North-East Atlantic
NEWP	Northeast Water Polynya
NGO	Non-Governmental Organisation
NIC	National Ice Centre (USA)
nm	nautical miles
NSDW	Norwegian Sea Deep Water
NWA	North-West Atlantic
OSPAR	OSPAR Convention (formerly Oslo and Paris Conventions) for the Protection of the Marine Environment of the North-East Atlantic
PAP	Porcupine Seabight Abyssal Plain
pers. com.	personal communication
PIK	Potsdam Institute for Climate Impact Research
POM	Particulate Organic Matter
PSA	Particular Sensitive Areas (of the IMO)
RAMSAR	RAMSAR-Convention on Wetlands of International Importance
SAR	Seas At Risk
UNCLOS	United Nations Convention on the Law of the Sea
UNEP	United Nations Environment Program
UNESCO	United Nations Educational, Scientific and Cultural Organisation
WB	World Bank
WCMC	World Conservation Monitoring Centre
WWF	WorldWide Fund for Nature (in North America: World Wildlife Fund)

Preface

The Convention on Biological Diversity (CBD, Rio de Janeiro 1992) was a major step forward in public recognition of the global scale of loss of biodiversity and the global need to protect and conserve natural values. This in turn led to greater awareness of nature conservation problems and together with ongoing scientific debates and initiatives, resulted in decisions within international organisations. On 23 July 1998 the ministerial meeting of Contracting Parties to the OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic adopted a new Annex V to the OSPAR Convention at Sintra/Portugal. Besides programmes of the OSPAR Commission for the prevention from pollution with hazardous and dangerous substances and the input of nutrients this new Annex V aims together with the Appendix 3 *inter alia* for the establishment of a representative system of Marine Protected Areas (MPAs) within the OSPAR Maritime Area.

Germany agreed to act as lead country for the establishment of such an OSPAR MPA system. The work started with a workshop on the Isle of Vilm, a branch office of the German Federal Agency for Nature Conservation (Germany, 1998). The participating experts agreed *inter alia* on "Draft Criteria for the Identification and Selection of Marine Protected Areas" and "Draft Guidelines for the Management of Marine Protected Areas". During the workshop it was also agreed that MPAs should not only protect marine species and habitats under immediate threat or which are subject to rapid decline, but MPAs may also aim to protect or conserve additional features, such as representativity, productivity and high natural biodiversity. Some of these ideas needed to be further elaborated, *e.g.* representativity requires the identification of broad sub-divisions of the OSPAR Maritime Area on biological and hydrographical basis. Therefore the German Federal Agency for Nature Conservation conducted this study to identify biogeographical units of the North-East Atlantic and Arctic Oceans with relevance for the OSPAR Maritime Area.

Measures like the OSPAR MPA process are particularly pressing according to the present situation of loss and change of marine biodiversity, and according to the related urgent call by the OSPAR Convention for action to protect, conserve, and restore marine biological diversity against increasing anthropogenic threats.

Prof. Dr. Hartmut Vogtmann
President of the Federal Agency for Nature Conservation

1 Introduction

or *"why trying to draw lines in the water?"*

Anthropogenic threats to marine biodiversity and the need for marine nature conservation have been emphasised in science (*e.g.* HAYDEN et al. 1984; MITCHELL 1987; SHERMAN and ALEXANDER 1986, 1989; GRASSLE 1991; THIEL 1992; ANGEL 1993; PRICE and HUMPHREY 1993; AGARDY 1994; GJØSÆTER 1994; SCOR 1994; SUCHANEK 1994; MERRET and HAEDRICH 1997; TICKELL 1997; ZEZINA 1997; HISCOCK 1997, 1998; KOSLOW and GOWLETT-HOLMES 1998; MULLINEAUX et al. 1998; GUBBAY 1988, 1995, 1999; KOSLOW et al. 1999; ROGERS 1994, 1999; THIEL and KOSLOW 1999) and also for a long time by NGOs (*e.g.* GREENPEACE; SAR; WCMC; WWF) but action for the establishment of marine protected areas is still in its infancy, despite the promotion of such initiatives on a global scale by the GBRMPA together with the WB and the IUCN already in 1995 (KELLEHER et al. 1995) or within the MAB-program in 1981 (RAY et al. 1981) or independent initiatives. First steps towards a representative system of coastal and marine protected areas in Europe were successfully taken by the HELCOM in 1994 in the programme for BSPAs (HELCOM 1994).

The threats from fisheries – exploiting the oceans horizontally on a global scale and to an increasing extent even vertically –, increasing pressure on coastal and even offshore areas for commercial use, continuing threat of contamination with nutrients and pollutants, and the fear for future commercial activities on shelves, seamounts, and even in the deep-seas makes it urgent to make progress with marine nature protection measures.

To fulfil demands of the "Convention on Biological Diversity", it is necessary to distinguish different biogeographical areas as a basis for the protection of marine biodiversity and ecosystems and to get representativeness of biodiversity on a higher scale of a zonation and regionalization above the level of habitats, biocoenoses, and species.
Representativeness within a biogeographic region is a commonly used criterion for the identification, selection, and designation of MPAs by most institutions and programmes involved in such tasks *e.g.* EU/NATURA; IMO/PSAs; HELCOM/BSPAs; IUCN [HAYDEN et al. 1984, KELLEHER et al. 1995]; JNCC (*e.g.* HISCOCK 1998); N.COUNC.; OSPAR Convention Annex V/Strategy on the Protection and Conservation of the Ecosystems and Biological Diversity of the Maritime Area 1998; RAMSAR; WWF Canada (DAY and ROFF 1999, ROFF and TAYLOR 2000); (BELBIN 1993).
Therefore practical and useful biogeographic units of the vast OSPAR Maritime Area needed to be identified, to make the aims of the declaration operational. For this reason this study has been undertaken on behalf of the German Federal Agency for Nature Conservation to identify biogeographical units in the OSPAR area. The results have been illustrated on (schematic) maps and have been presented, discussed, and adopted at the 1999 OSPAR workshop at Oban/Scotland and further modified submitted to OSPAR-IMPACT at Brest/ France (1999), presented again at the 2nd OSPAR workshop on habitat classification at Southampton/England in September 2000 and – as being *i.a.* one base for marine nature conservation – presented also on the 2nd OSPAR workshop on MPAs on the Isle of Vilm/Germany in June 2000.

This report is the outcome of the research, various discussions, and revisions. It might not fulfil pure requirements of *e.g.* statistical and taxonomic approaches concerning this matter in all aspects but it is a biogeographic approach which integrates different biogeographic concepts and which simplifies vertical zonation patterns for use within the OSPAR MPA-process to produce practical and useful units for this task.

To provide such a tool was particular pressing according to the present situation regarding loss and change of marine biodiversity and the related urgent call by Annex V/Appendix 3 of the OSPAR Convention for action to protect, conserve and restore marine biological diversity against increasing anthropogenic threats.

Special gratitude is expressed to Prof. Dr. Brattegard (Norway), Dr. Gubbay (UK), and Prof. Dr. Thiel (Germany) for their critical review of and valuable comments on the manuscript, and to Prof. Dr. Glémarec (France) for comments and his permission to use his partly unpublished maps and data.

2 The OSPAR Maritime Area

The entire OSPAR area comprises the Maritime Area as well as the hydraulic system of streams and their catchments. As this study is only concerned with marine biogeography any mentions of the OSPAR area in this study refer to just the OSPAR Maritime Area.
This area comprises the inner and territorial waters of the OSPAR contracting parties as well as the adjacent EEZs and high seas including the seabed and its subsoils within the following boundaries (OSPAR–ASMO 1994, 1997) (Fig. 1):
The north-east Atlantic and parts of the adjacent Arctic Ocean between 36°N and the North Pole and from 51°E to 44°W but excluding:

- the area between 44°W and 42°W from 36°N to 59°N.
- the Baltic Sea and Belts south and east from lines between Hassensørhoved and Gniben and between Gilbjerghoved to Kullen. There applies the Helsinki Convention.
- the Mediterranean and its dependent seas as far as the point of intersection of 36°N and 5°36'W. There applies the Barcelona Convention.

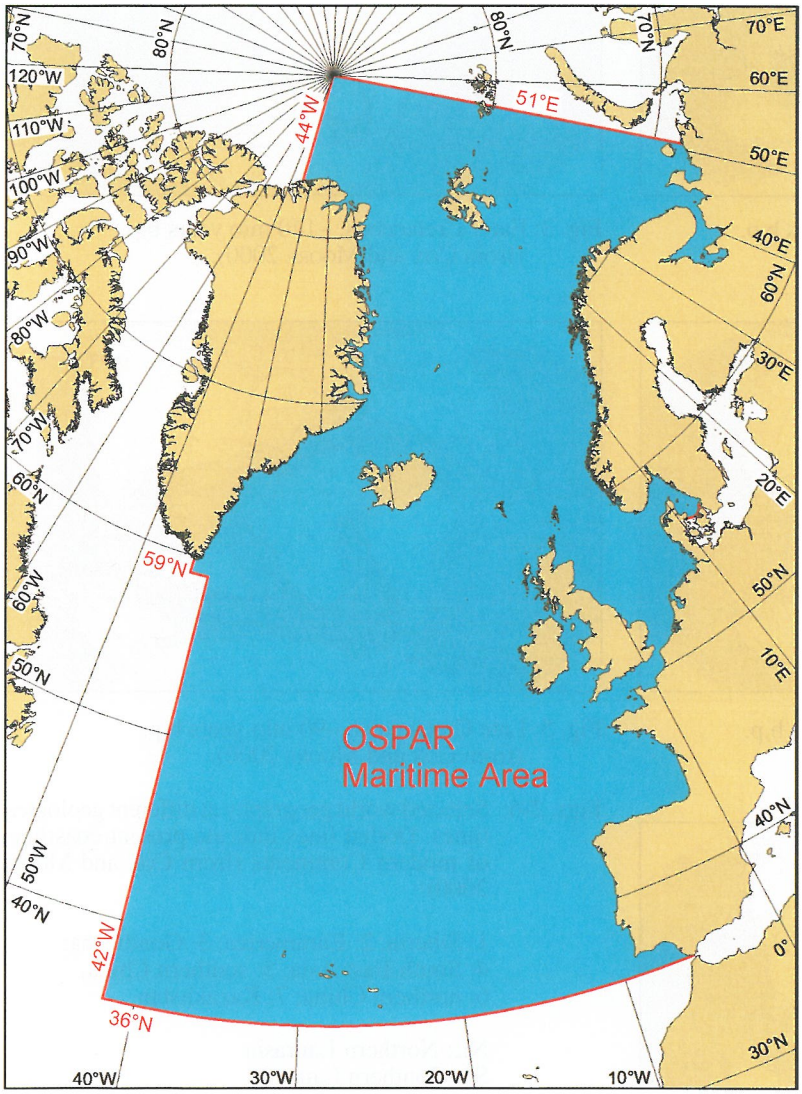


Fig. 1: Stereographic projection of the North-East Atlantic and adjacent Arctic waters showing the extension and boundaries of the OSPAR Maritime Area.
The N-S expansion of the OSPAR area exceeds 6,000 km.

3 Oceanographic Settings of the North-East Atlantic

3.1 Geology

Despite earlier biological significance, it was only in the 1960s when Alfred L. Wegener's continental drift theory – published in various treatises between 1912-1929 – was confirmed by palaeomagnetic seafloor data and thus widely accepted by the scientific community. Plate-tectonics were a revolution for geology but as well for explanatory models of terrestrial and marine biogeographic patterns (Gray and Boucot 1979). On the other hand fossils in biostratigraphic records were used to confirm tectono-geological assumptions and also to outline palaeobiogeographical concepts (Hallam 1973, 1981; Pielou 1979; Briggs 1987,1995).

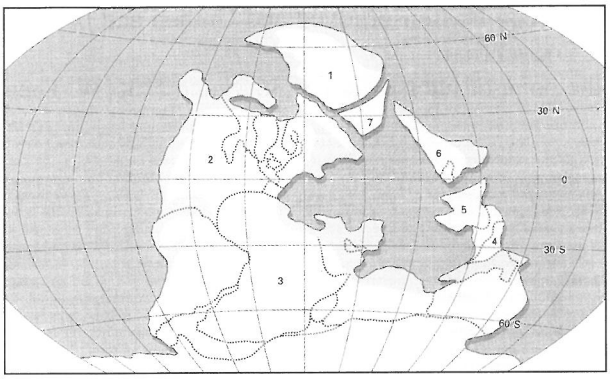


Fig. 2: Late Carboniferous, ~280 mio years b.p. (from Cox and Moore 2000).

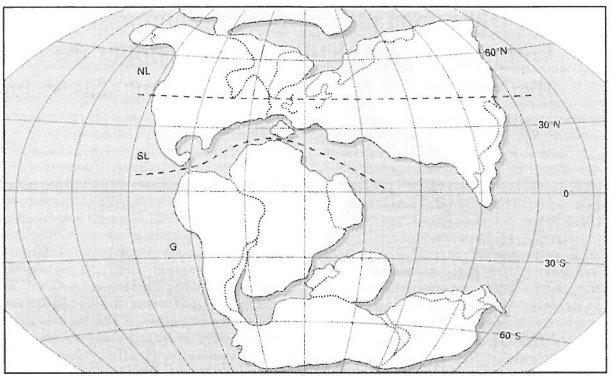


Fig. 3: Early Cretaceous, ~140 mio years b.p. (from Cox and Moore 2000).

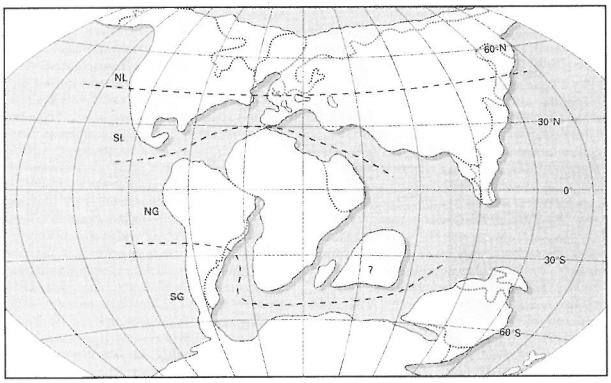


Fig. 4: Middle Cretaceous, ~105 mio years b.p. (from Cox and Moore 2000).

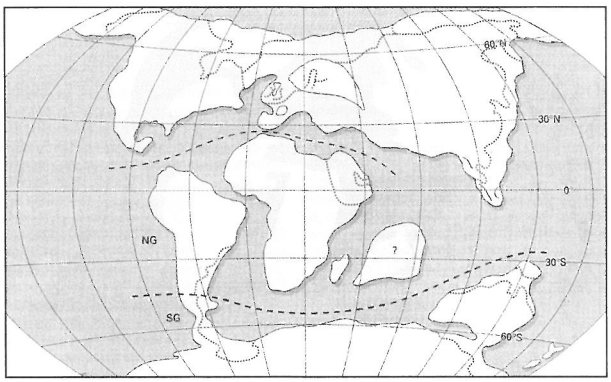


Fig. 5: Late Cretaceous, ~90 mio years b.p. (from Cox and Moore 2000).

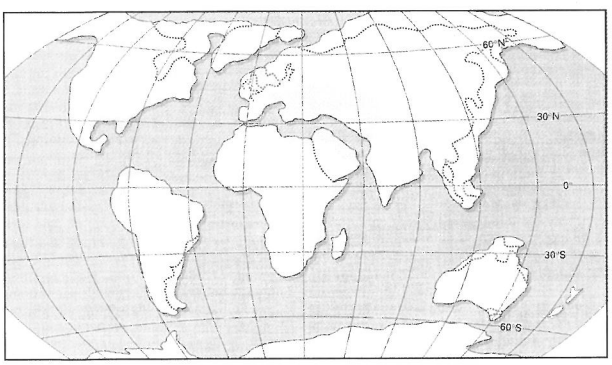


Fig. 6: Eocene, ~40 mio years b.p. (from Cox and Moore 2000).

Figs. 2-6: Selected world geography at different geological times. Dotted lines indicate present coastlines of modern Continents (from Cox and Moore 2000):

1: Siberia; 2: Euramerica; 3: Gondwana;
4: South-East Asia; 5: southern China;
6: northern China; 7: Kazakhstan

NL: Northern Laurasia
SL: Southern Laurasia
G: Gondwana
NG: Northern Gondwana
SG: Southern Gondwana

The Atlantic did not exist until ~165 mio years ago when seafloor spreading started to divide southern Gondwana during the Jurassic with a main formation of the Atlantic during the Cretaceous (Figs. 3-5) (SCLATER and TAPSCOTT 1979). This – in geological terms – relative young age did not provide much time for evolutionary differentiation and speciation and thus makes biogeographic approaches using endemism rates more difficult for the Atlantic compared to other oceans. VERMEIJ (1991) estimated that the diversity of molluscs is 1.9 times higher in the cool-temperate Pacific than in the Atlantic, EKMAN (1953) estimated a six- to eightfold higher biotic diversity in the Pacific, whereas BRIGGS (1970) estimated a ratio of 3:1 for fishes in favour of the Pacific.
Within the Atlantic the South Atlantic had been separated by the tropical ocean corridor of the Tethys from the northern Atlantic in the Cretaceous (Figs. 3-6). The development of the northern Atlantic had advanced only in the Tertiary with the formation of the Norwegian-Greenland basin during the Palaeocene and Eocene and a first connection to the Arctic ocean (Figs. 3-7) (SCLATER et al. 1977; GRAY and BOUCOT 1979; THIEDE 1980; COX and MOORE 2000).

The Arctic, being the youngest ocean, was separated from the Atlantic by two landbridges – the "Thulian route" from Labrador and Baffin Island through southern Greenland and Faeroes Island to Scotland, and the "DeGeer route" from Ellesmere Island through northern Greenland, Spitzbergen to Scandinavia – until the Eocene (BOTT et al. 1983; BRIGGS 1987; COX and MOORE 2000). A deep water connection between the Arctic and Norwegian-Greenland basins was not established before the Oligocene/Miocene (THIEDE 1980; THIEDE et al. 1989; THIEDE et al. 1990). The northernmost part of the OSPAR area is part of the Eurasian Basin of the Arctic Ocean which developed within the same period as the North Atlantic (CHURKIN and TREXLER 1981). According to later authors there had been multiple plate collisions that formed land bridges across the present Bering Strait and isolated the Arctic basin between the early Cretaceous (~125 mio years b.p.) and the Eocene (~50 mio years b.p.). The Nansen (Gakkel) Ridge (see Fig. 107) depicts the Arctic extension of the Mid-Atlantic Ridge (MAR) and is one of the four prominent elevations rising from the Arctic Ocean floor. The Eurasian Basin development is related to the one of the North Atlantic Basin mainly as a Cenozoic phenomenon (63-40 mio a ago) but with evidence for the geological record since the later Mesozoic era (HERMAN 1974; VOGT and AVERY 1974; CLARK 1975; DAWES AND PEEL 1981; THIEDE et al. 1990) while the Amerasian Basin might have developed from the Palaeozoic on. For this basin are more precise data available.

Further geological developments in the Tertiary closed the isthmuses of Panama, Anatolia-Arabia, and the Bering Strait causing major changes in surface and deep water circulation of the oceans (VALENTINE 1973; VALENTINE and MOORES 1974; VAN ANDEL 1979; COX and MOORE 2000).
The Panamanian isthmus which existed until ~2 mio years ago (HAQ 1984) was a Atlanto-Pacific shallow water connection at later stages allowing species interchange only for epipelagial tropical faunas thus resulting in closer taxonomic similarity than for mid- or northern latitude counterparts (VAN DER SPOEL and HEYMAN 1983) or for meso- or bathypelgic faunas, respectively. These could not cross over (ANGEL 1993). BRIGGS (1974) gave only a rate of 1% for fish species shared by both oceans.
The Bering Strait was finally reopened ~3.5 mio years ago in the Pliocene and allowed the interchange of cool temperate and polar marine species with a massive dominance of Pacific invaders (at least for molluscs) (HØISAETER 1986; VERMEIJ 1991, 1992; GLÉMAREC pers.com).

Fossil records enable the reconstruction of palaeobiogeographic patterns. Mollusc shells are often well preserved in sediments and are thus especially valuable indicators in their biogeographic response according to their benthic ecological niche (*e.g.* VERMEIJ 1989, 1991, 1992). However for the pelagic skeletal bearing taxa as diatoms, foraminifers, radiolarians, coccolithophorids, silicoflagellates, and pteropods only foraminifers have been studied extensively in the past (ANGEL 1993) (compare also Fig. 93). An example for Cretaceous bivalve distribution patterns is given by KAUFFMAN (1973), who differentiated Thetyan and northern and southern temperate realms with different regions, provinces, subprovinces, and endemic centres (Fig. 7). No cold water and Arctic bivalves and therefore no such provinces are known from the Cretaceous (KAUFFMAN 1973).

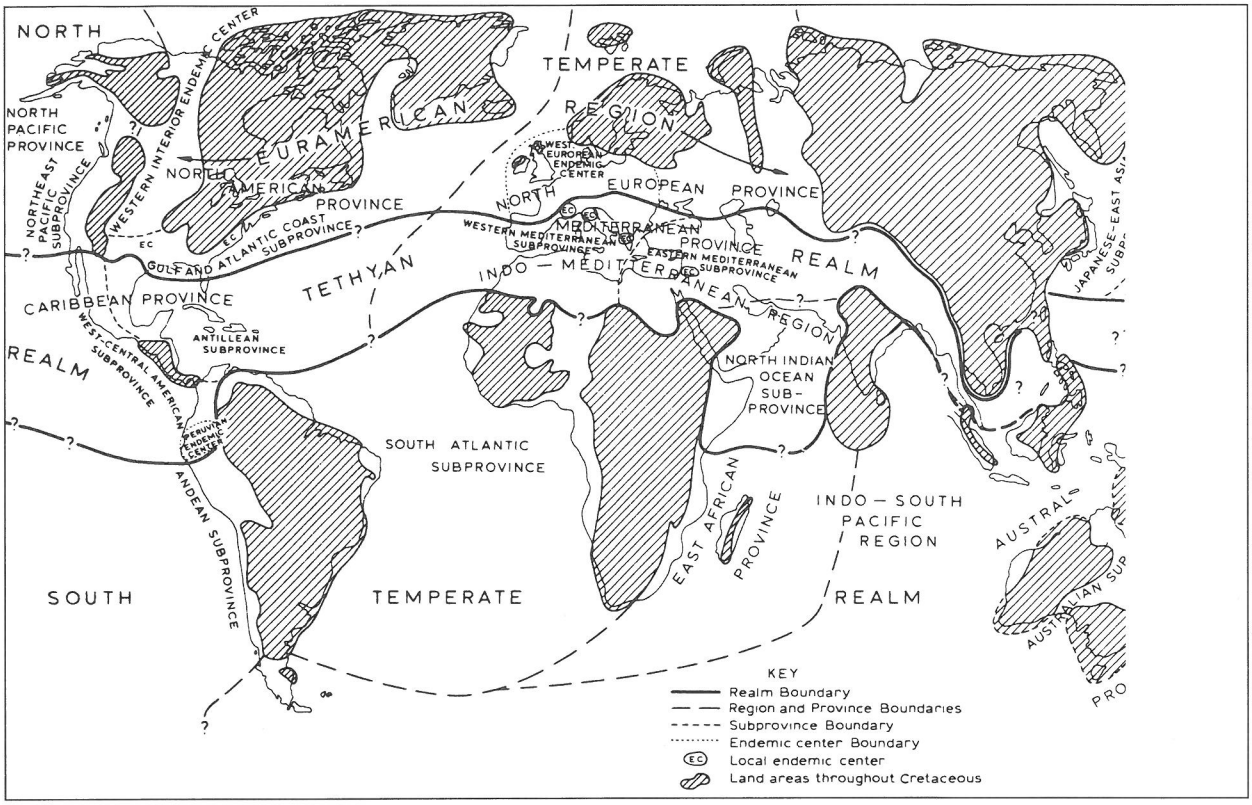


Fig. 7: Average distribution of Cretaceous biogeographic units based on bivalves – realms, provinces, subprovinces, and endemic centres in decreasing order of magnitude – plotted against the present global configuration of continents and seas (from KAUFFMAN 1973).

The Mid-Atlantic Ridge (MAR) as a seafloor spreading centre has separated the American from the Eurasian plate. The age of the seafloor is therefore increasing from the MAR in the centre to the peripheral continental margins (NICOLAS 1995). Oceanic islands (*e.g.* Azores, Jan Mayen), seamounts, hydrothermal vents (HTV), and other topographical features are the results of volcanic and spreading processes mainly from Cenozoic times. EPP and SMOOT (1989) counted as many as 810 seamounts with a relief greater than 50 fathoms (≈92 m) resulting from geological hotspot/volcanic processes related to seafloor spreading in the North Atlantic between ~5°-62°N and presumed many more to be buried under deep-sea sediments. Within the OSPAR area there are clusters of seamounts along the Azores-Biscay Rise (Charcot Seamounts), Azores-Portugal Rise (Horseshoe Seamounts), and the Madeira-Tore Rise, off N- and NW-Iberia (*e.g.* Biscay Seamounts, Dôme Cantabria, Dôme Gascogne), along the longitudinal structures of the MAR, west of the MAR (Milne Seamounts) (VIGNEAUX 1974; EPP and SMOOT 1989) besides the better known topographic features in the region around the Rockall plateau (compare Figs. 10, 107). There are also seamounts in the northern basins *e.g.* one very prominent seamount at ~73°30'N/9°W and widely spaced clusters of seamounts separated by long stretches of sediment-filled valley floor as parts of the Knipovich Ridge. Seamounts are supposed to be extremely important for biological processes and patterns in deep sea environments (Chap. 6.3.3).

About 60-35 mio years ago the Azores-Biscay Rise depicted the Iberian-African and Eurasian plate boundary whereas today the African-Eurasian plate boundary runs from the Azores Triple Junction eastwards along the Azores-Portugal Rise (EPP and SMOOT 1989). Transversal fracture zones (*e.g.* Charlie Gibbs and Jan Mayen Fracture Zones) and aseismic ridges (*e.g.* Iceland-Faeroe Ridge), and gashes (*e.g.* King's Trough) disturb the longitudinal symmetry of the North Atlantic sea floor (compare Figs. 10, 107) (SCLATER and TAPSCOTT 1979; NICOLAS 1995).

The MAR continues north of Iceland in more differentiated structures, with the Kolbeinsey, Jan Mayen, Mohns, and Knipovich Ridges and additional features in the Norwegian-Greenland basin and the Nansen (Gakkel) Ridge in the Arctic basin as a further successor (compare Fig. 107).

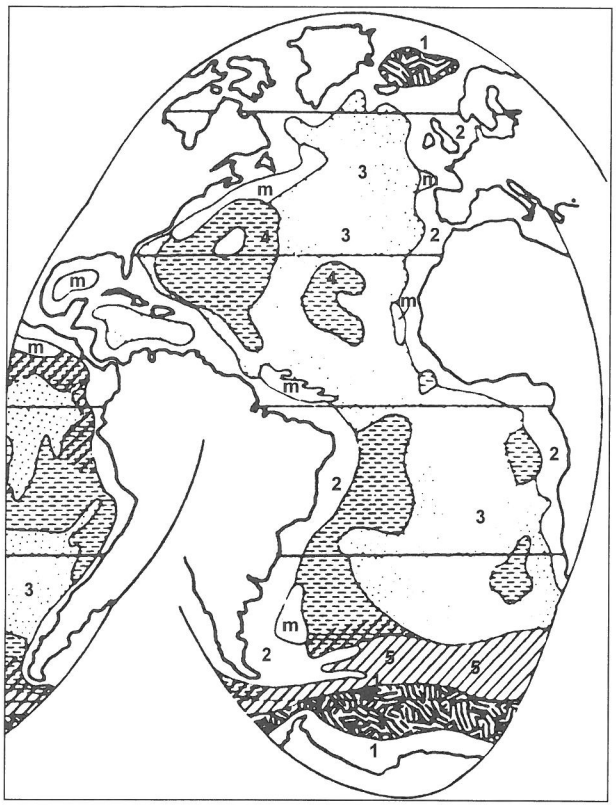


Fig. 8: Distribution of recent sediments on the ocean floor (from BERGER 1974).
1: glacial debris; 2: shelf and slope deposits;
3: calcareous ooze; 4: clay or no deposit;
5: siliceous ooze; m: deep-sea muds

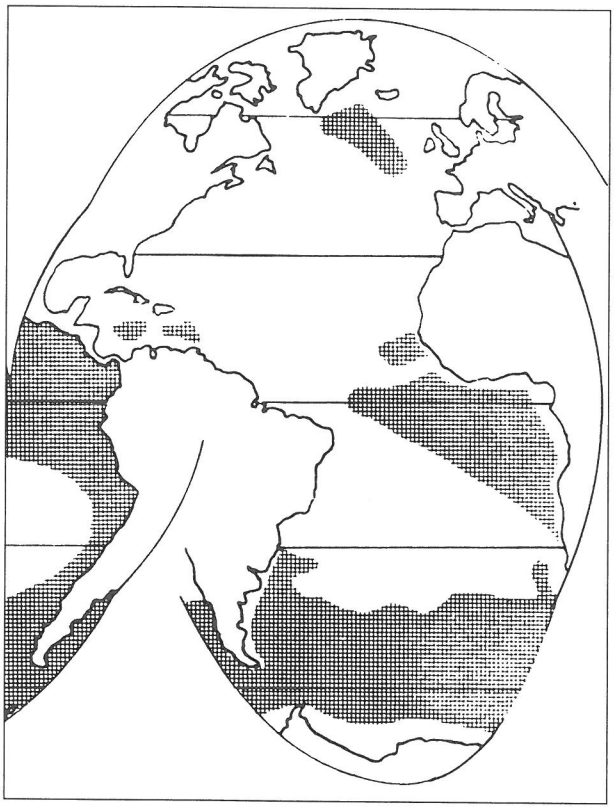


Fig. 9: Areas with abundant siliceous deep-sea deposits (from BERGER 1974).

The ocean floor is covered by massive layers of soft sediments. Beyond the continental slope and rise, and after transition from terrigeneous to oceanic/pelagic origin, the sediments are dominated by calcareous ooze (globigerina and pteropod shells) and Illite as dominant clay mineral within the OSPAR area (Fig. 8) (BERGER 1974), forming flat abyssal plains (SCLATER and TAPSCOTT 1979). Oceanic sediments can be classified in different categories of eupelagic and hemipelagic deposits (BERGER 1974; EINSELE 1992) with further regional differentiation depending on the different productivities in the surface layer (see Chap. 6.3.1.).
There is a calcium carbonate compensation depth (CCD) and a lysocline at depths between 4.5 and 5 km, respectively. Below this level pelagic snowfall of calcareous sediments dissolves rather than accumulates because water is undersaturated with calcium carbonate thus leaving red clay as predominant material on deep ocean floors in regions with oligotrophic surface waters (BERGER 1974; SCLATER and TAPSCOTT 1979; EINSELE 1992). These are rare within the OSPAR area. Siliceous deposits as diatom oozes occur mainly at high latitudes, diatom muds are typical for pericontinental regions, whereas radiolarian oozes dominate at equatorial areas (Fig. 9) (BERGER 1974; EINSELE 1992).
Near continental margins (hemipelagic) sediments might be covered by layers of detrital material (clay and sand interspersed with calcareous ooze and organic matter) that has spilled from the continental shelves (BERGER 1974; SCLATER and TAPSCOTT 1979). Gravity mass flows form a great portion of sediment deposits downstream from continental slopes. Such moves might occur as slides, flows, slumps, or turbidity currents probably creating submarine canyons and huge deep-sea fans possibly reaching as far out as 1000 km into the oceans (EINSELE 1992).
In zones of upwelling the overall sedimentation of biogenic carbonate, silica, and particularly organic matter increases considerably due to higher biological production in surface waters compared to areas of normal fertility and the oxygen minimum layer might sink to the sea floor. Typical black shale and laminated sediments can develop under such induced reducing conditions below areas of upwelling (EINSELE 1992).

The crests of the MAR consist mostly of hard volcanic rock whereas the flanks are covered with an increasing vertical extension of soft sediments with increasing distance from the crests (SCLATER and TAPSCOTT 1979).

Only comparatively low concentrations of ferromanganese concretions (manganese nodules) can be found on the southern abyssal plains of the OSPAR area (BERGER 1974; BETT pers. com.).

3.2 Bathymetry and vertical subdivision

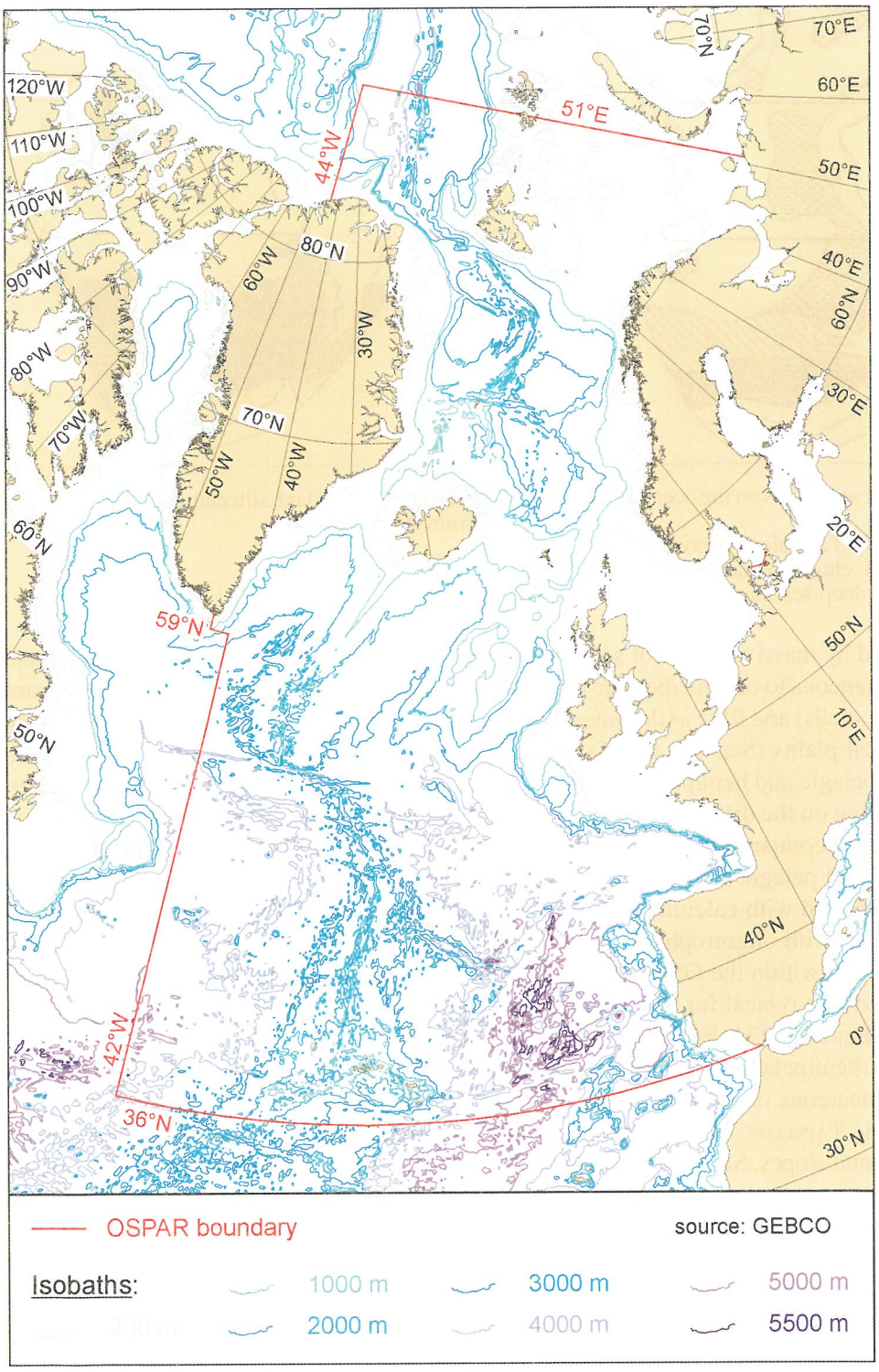


Fig. 10: Bathymetry of the North Atlantic and adjacent Arctic waters. Boundaries of the OSPAR Maritime Area are indicated.

The MAR, separating the Eurasian from the American plate as a still active seafloor spreading centre, is the striking meridional submarine elevation that divides the entire Atlantic ocean floor "symmetrically" with an average summit/crest depth of 2,500 m (Fig. 10). The Azores Triple Junction at the southern OSPAR boundary is a volcanic active geological junction of the MAR and the nowadays less active Azores-Portugal-Rise system which separates the Eurasian from the African plate (Chap. 3.1) (see also Fig. 107). In the OSPAR area the MAR – called Reykjanes Ridge in its northern part – separates the Newfoundland and Labrador basins from the West-European basin, and the Irminger from the Iceland basins. North of Iceland it continues as Kolbeinsey Ridge, Mohns Ridge, and Knipovich Ridge segregating the Greenland basin from the Norwegian and Lofoten basins, further continuing as Nansen Ridge in the Arctic Ocean separating the Fram and Nansen basins.
The MAR, further submarine rises and ridges, several seamounts and banks (Chap. 3.1), and oceanic islands of volcanic origin (*e.g.* Azores and Jan Mayen), all rising up from bathyal and abyssal depth, and troughs in-between give the seafloor of the OSPAR area a much more differentiated submarine topography (see Figs. 10, 107) than typical illustrations of the vertical ecological structure of the oceans (*e.g.* Fig. 12). In addition to the topographical features mentioned above there are also rías and submarine canyons indented into the continental slope at several locations (*e.g.* Portimão, São Vincente, Setúbal, Lisboa-Tejo, and Nazaré Canyons/ Portugal; Avilés, Lastres, Torrelavega, Santander Canyons/Spain; Gouf du Cap Breton, Cap-Ferret Canyon/ France – the later six in the Bay of Biscay, or within the Porcupine Seabight off the Celtic Shelf break).

In the OSPAR area abyssal depths extend down to ≥ 5500 m in the West-European and Newfoundland basins (Fig. 10).

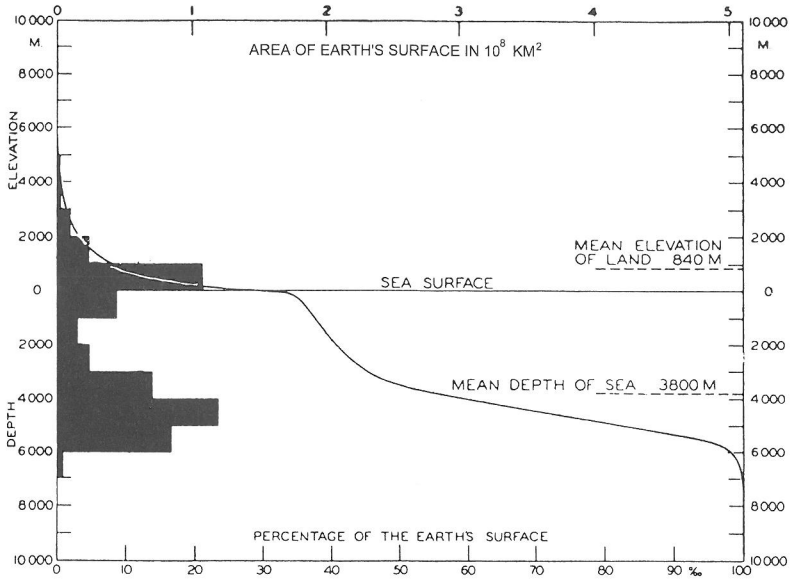


Fig. 11: Hypsographic curve: Overall depth distribution of the ocean floor and land elevations; left block scheme: Frequency distribution of elevations (from SEIBOLD and BERGER 1983).

The figure 11 shows the overall depth distribution of the world ocean floor and the frequency distribution of the world's land and ocean elevations. Mean depth and depth distribution in the OSPAR area is not as great with a smaller deep-abyssal proportion but the scheme still visualises the proportions between deep-sea areas > 1000 m and shallow areas < 1000 m fairly well.

The vertical ecological structure of the oceans as shown in figure 12 is a generalised sketch of the real proportions. The oceanic areas and thus the holopelagial and the abyssal plains are much more extensive compared to the continental margin structures (see Fig. 11).
Regarding the pelagial and the benthal as the main ocean realms there are further vertical subdivisions common that have ecological relevance for marine life.
The depth of the epipelagial (and mesopelagial) zone varies considerably depending on the intensity and depth of light penetration into the water which is differently decreasing in its spectral constituents with increasing depth. The upper epipelagial is the phytal of the pelagic realm. Light penetration depends on

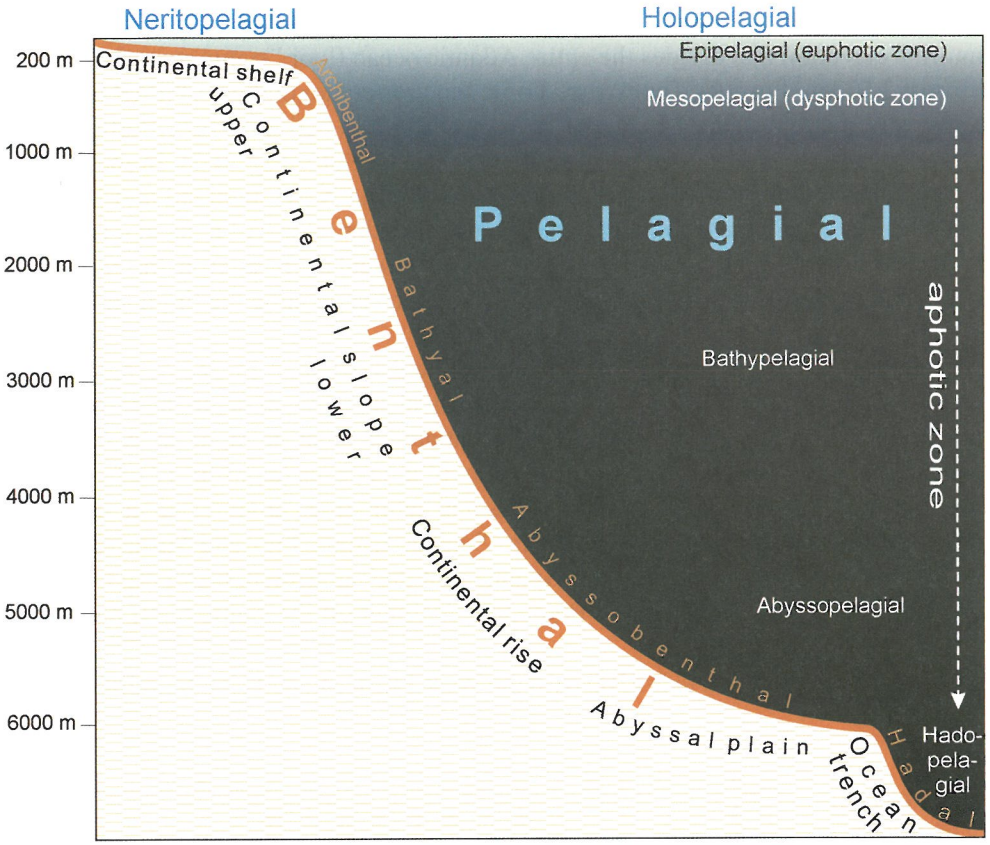


Fig. 12: Scheme of the vertical ecological structure of the ocean (after various sources; horizontally not drawn to scale). The oceanic areas and thus the holopelagial and the abyssal plains are much more extensive compared to the continental margin structures. Within the OSPAR area there is no trench (ultraabyssal/hadal) within the entire North Atlantic and Arctic oceans. Abyssal depths are reaching down to ≥ 5500 m in the OSPAR area (compare Fig. 10). The submarine relief is furthermore characterised by the MAR, further rises and ridges, seamounts, and oceanic islands rising up from the deep ocean floor.

latitude and therefore on the angle of radiation income and seasonality (Chap. 3.4) as well as on water cloudiness caused by the concentration of particulate organic and inorganic matter (and thus by the trophic situation) induced by thermohaline circulations, turbidity fronts, upwellings, and mixed water input from the continental shelves (Chap. 3.3). In lower latitudes the epipelagial of "blue water" areas may reach as deep as 600 m.

The mesopelagial zone is defined as the dysphotic twilight zone below which very small but still measurable light quantities penetrate. Its depth thus depends on epipelagial water transparency above with a maximum depth of ~1200 m (Fig. 12) and nutrition depending on trophic input from above by sinking of faecal material and dead organism bodies or transport by vertically migrating animals. Vertical migration by the animals of the pelagic realm integrates trophodynamic processes within these communities in the vertical plane. The mesopelagic realm is almost absent from the cold polar seas (Backus et al. 1977; van der Spoel and Heyman 1983). Since some pelagic organisms seem to be rather more temperature sensitive than light orientated some authors have proposed a scheme combining temperature and depth latitudinally to describe vertical boundaries in the pelagial at different latitudes (Fig. 13) and also related to the phenomenon of polar emergence and equatorial submergence (Fig. 14) (*e.g.* van der Spoel and Heyman 1983).

The aphotic bathypelagial and abyssopelagial are completely devoid of visible radiation, species abundance and biomass are severely reduced, migration is low due to energy saving as being a cardinal principle, and nutrition depends on detrital snow and large food falls. There is a benthic boundary layer (BBL) (± ~100 m) in which bathypelagic and abyssopelagic organisms are more or less closely related to the ocean floor (Gage and Tyler 1991).

The distribution and abundance of meso- and bathypelagic zooplankton can present special features in the near bottom waters of the continental slope and in submarine canyons, where these oceanic species may accumulate due to the depth of their preferred diurnal biotope (MAYCAS et al. 1999).
In the Holopelagial the epipelagic fauna is largely dominated by phytophagous filter-feeders, the mesopelagial is inhabited mainly by carnivorous and euryphagous taxa, while detritus-feeders dominate the depth (VAN DER SPOEL and HEYMAN 1983; VINOGRADOV 1968).

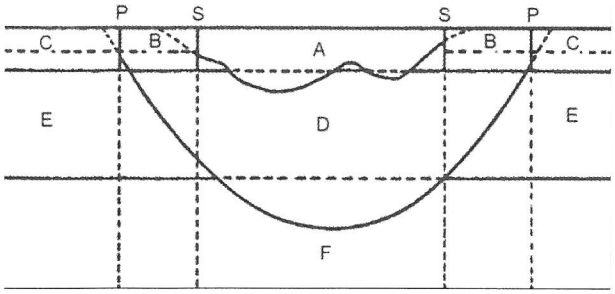


Fig. 13: Vertical north-south cross-section through a hypothetical ocean with different pelagic biotopes (from VAN DER SPOEL and HEYMAN 1983):
A = epipelagic: between Subtropical fronts, surface and 15°C isotherm
B = epiboreal-pelagic: between Subtropical and Polar fronts, surface and 200 m depth
C = epipolar-pelagic: polewards of Polar fronts, between 0 and 200 m depth
D = mesopelagic: below 200 m or below 15°C isotherm
E = mesopolar-pelagic: below 200 m or below 5°C isotherm
F = bathypelagic: below 1000 m or below 5°C isotherm
P = Polar Front;
S = Subtropical Front

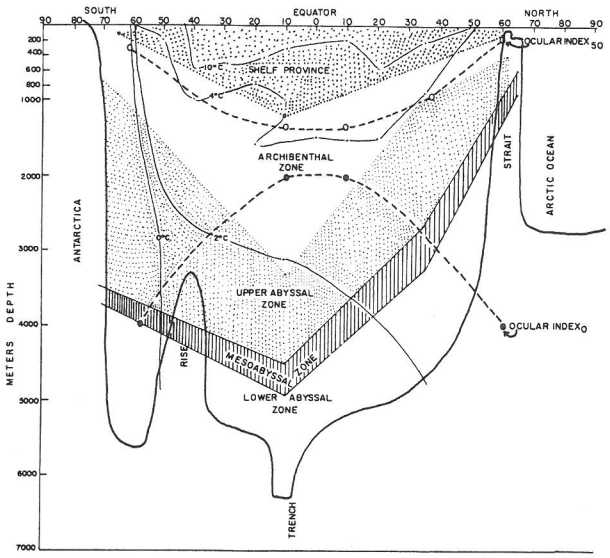


Fig. 14: Depth distribution of faunal zones, selected isotherms, and ocular indexes plotted along an imaginary north-south section of an ocean (data from the Pacific) (from MENZIES et al. 1973, modified).

The vertical zonation of globally spread benthic and pelagic organisms might change frequently with latitude. Coldwater species show the phenomenon of polar emergence and tropical submergence related to the vertical shifting of isotherms in thermal étages (Figs. 13, 14) (*e.g.* LE DANOIS 1948; ZENKEVITCH 1948/1949; EKMAN 1953; HEDGPETH 1957; DE LATTIN 1967; VINOGRADOV 1968; MENZIES et al. 1973; VAN DER SPOEL and HEYMAN 1983; GLÉMAREC 1973, 1988; VINOGRADOVA 1997; ZEZINA 1997; LONGHURST 1998). When the disappearance of taxa from surface waters or vertical shifting in other water masses occurs at about the polar or subpolar fronts, the term tropical/equatorial submergence is not adequate.

In almost all the mediterranean seas (as *e.g.* the Arctic Ocean) and certain marginal seas the physicochemical features of the intermediate and deep waters differ considerably from those of the oceans resulting in different deep pelagic biocoenoses (VINOGRADOV 1968).
Pressure increases at a rate of ~1 atmosphere for each 10 m of depth, and thus might affect the distributions of organisms because special adaptations are needed to survive in these different environments. Organisms containing air-filled organs (*e.g.* the swim bladders of fish and lungs of sea mammals) are strongly affected by such changes. Organisms adapted to life at great depths may have very soft bodies (they don't need hard shells to keep them stiff at these great depths due to hydrostatic pressure), which may cause problems for them if transported to shallower habitats. However, many soft bodied invertebrates are surprisingly tolerant of changes in pressure. Further factors affecting the vertical and horizontal distribution of deep-sea animals are discussed in the chapters 3.1-3.5.1.; 4.2-4.4; and 6.1-6.3.3.

Concerning the benthic realm there is still a frequent input of particulate organic matter (POM) horizontally from the shelf to archibenthal depths and more rarely to bathyal zones of continental slopes (see Chap. 3.1), whereas the abyssobenthal depends completely on POM as food source and some rare larger carcasses. Deep-sea HTV and cold seep biocoenoses are exceptions from this situation.

Vertical delimitations for benthic deep-sea zones have been given a variety of names. Some of these were listed by MENZIES et al. (1973) and CARNEY et al. (1983). The former only differentiated the shelf (< 1000), an archibenthal zone of transition/AZT which shifts latitudinally from 12-360 m in the Arctic to ~450-950 m off the Carolinas/USA or 1000-2000 m in the Bay of Biscay, and the abyssal below. LE DANOIS (1948) distinguished *i.a.* sublittoral (30-90 m), neritic (90-200 m), Atlantic margin (200-1000 m), semiabyssal/ archibenthal (1000-2000 m), and Abyssal (2000-5000 m). HEDGPETH (1957a) used different zones above 250 m, bathyal (250-4000 m), and abyssal (4000-6000 m). Pérès (1957) subdivided the bathyal (200-3000 m) and abyssal (3000-6500 m) below different shallow zones. ZENKEVITCH (1963) differentiated surface sublittoral (0-200 m), transition (200-600 m), and abyssal (600-10,000 m) zones. Due to ZEZINA (1997) the bathyal stretches from 200 m to 3000 m with the abyssal continuing below due to VINOGRADOVA (1962). For the pelagial a vertical zonation was given by VINOGRADOV (1968) (Fig. 82) with epipelagial (0-150/200 m), transitional/mesopelagic layer (150/200-750/1000 m), bathypelagial (750/1000-2500/3000 m), and abyssopelagial (> 2500/3000 m). (Ultra-abyssal/hadal delimitations have not been taken into account above because they are lacking in the OSPAR area.)

The geomorphological shelf break can be substantially deeper, but also shallower than commonly quoted with 200 m. In the Arctic for example, the shelf break is mainly deeper around ~400-600 m and, at some locations, even 1000 m. At the south-western Portuguese coast the shelf has a comparably "sharp" edge at ~100 m with a step down to the 700 m contour. Off the southern Iberian Atlantic coast the shelf break is below 500 m, and at many volcanic islands there is virtually no shelf at all.
Apart from cold water regions (*e.g.* Arctic) the ecological vertical delimitations from the shelf break to 2500-3500 m for the bathyal and from there further downwards to 6000 m for the abyssal are usually used as shown in Figure 12. The term archibenthal has been abandoned by most deep-sea scientists despite the special and important ecological character of being a transition zone between the shallow and deep-sea fauna and ecosystems with a markedly change in depth, temperature range, sediments, and species composition and abundance (compare MENZIES et al. 1973).

3.3 Currents, water masses, upwelling regions, and fronts

Ocean circulation patterns have changed frequently since the break-up of Pangaea and the dispersal of continental fragments in the Panthalassa. BERGGREN and HOLLISTER (1977), HERMAN (1979), HAQ (1984), ANGEL (1994), and COX and MOORE (2000) presented maps that show past circulation patterns changing within the last 59 mio years. These maps show current patterns and regions of upwelling derived from evidence in geophysics and palaeontological research on marine sediments.
The present surface and deep water circulation and current patterns of the North Atlantic were established only after the formation of the circum-Antarctic circulation, the interruption of the circum-global equatorial seaway of the Tethys, together with the closure of the isthmuses of Panama, Anatolia-Arabia and the Bering Strait in the Tertiary with later being reopened in the Pliocene. VERMEIJ (1992) mentioned a (possible) velocity increase of equatorward eastern boundary currents as well as of the Gulf Stream and other Atlantic currents during the early Pliocene resulting from a shoaling and the ultimate closure of the central American seaway. This long period of inter-ocean connection of the Atlantic with other palaeo-oceans has resulted in a comparatively wide spreading and a low rate of differentiation of pelagic organisms (THIEDE 1980; COX and MOORE 2000).

From the maximum Pleistocene glacial situation ~18,000 years ago, current patterns have changed considerably with a shifting of isotherms, frontal zones and related biota up to 15°-20° of latitude northwards in the eastern Atlantic (Fig. 16) (*e.g.* BERGER 1974; VAN DEN HOEK 1975; VAN DER SPOEL and HEYMAN 1983; ANGEL 1993).

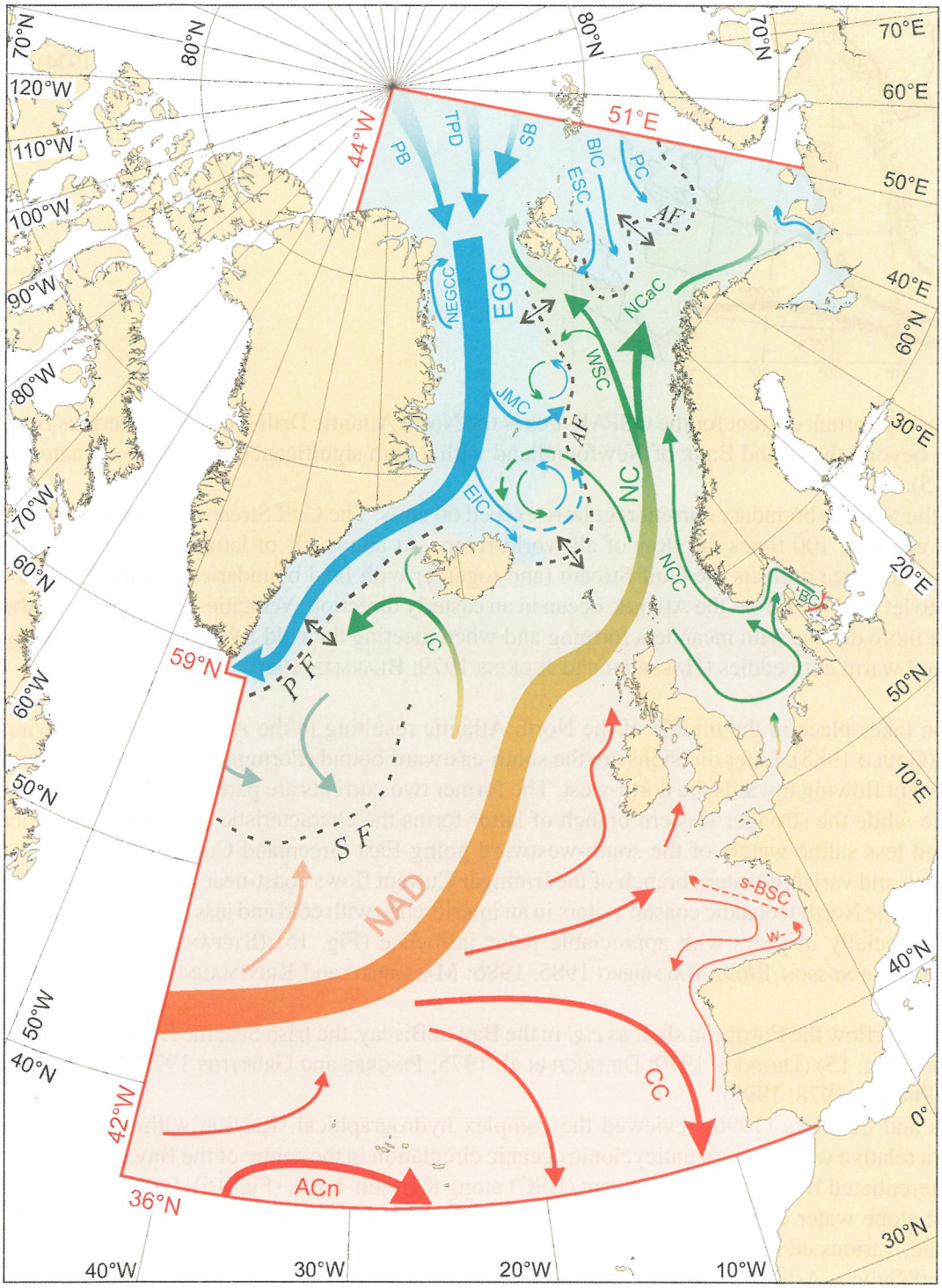


Fig. 15: Selected surface current patterns and oceanic fronts.

NAD	North Atlantic Drift	NEGCC	North-East Greenland Coastal Current
ACn	Azores Current northern branch	JMC	Jan Mayen Current
CC	Canary Current	EIC	East Iceland Current
BSC	Biscayan Slope Current	ESC	East Spitzbergen Current
	s-/summer, w-/winter	BIC	Bear Island Current
IC	Irminger Current	PC	Persey Current
NC	Norwegian Current	TPD	Transpolar Drift
NCaC	North Cape Current	PB	Polar Branch
WSC	West Spitzbergen Current	SB	Siberian Branch
BC	Baltic Current	*PF*	*Polar Front*
NCC	Norwegian Coastal Current	*AC*	*Arctic Front*
EGC	East Greenland Current	*SF*	*Subarctic Front*

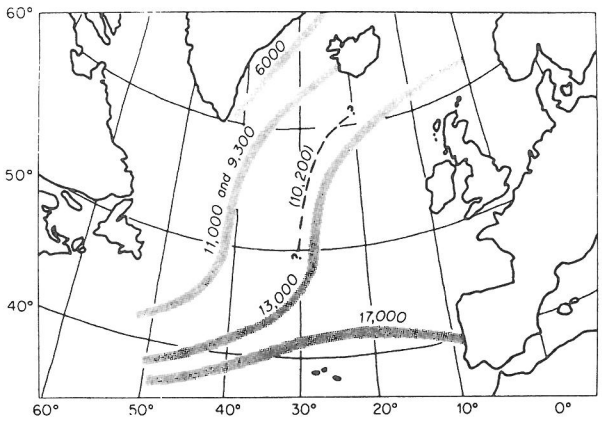


Fig. 16: Retreat of the polar front during deglaciation as recorded in deep-sea sediments, a prime example of climate transgression (from BERGER 1974).

Presently the most important current for the OSPAR area is the North Atlantic Drift (NAD) that derives from the Gulf Stream beyond the Grand Bank of Newfoundland with a high significance for marine climates of the NEA (Fig. 15).
The velocity of the western boundary current regularly exceed 60 cm/s. The Gulf Stream at Cape Hatteras is transporting for example 100 times the flow of all world rivers. At about 40° of latitude the geostrophic effect of the Coriolis force deflects the Gulf Stream (and together with land boundaries and the Labrador countercurrent) to let the NAD cross the Atlantic ocean in an easterly direction. Velocities slow down and the currents become more diffuse with meanders forming and when meeting the cold SW-going current, being cut off as cold and warm core eddies (HAEDRICH and JUDKINS 1979; BEARMAN 1989).

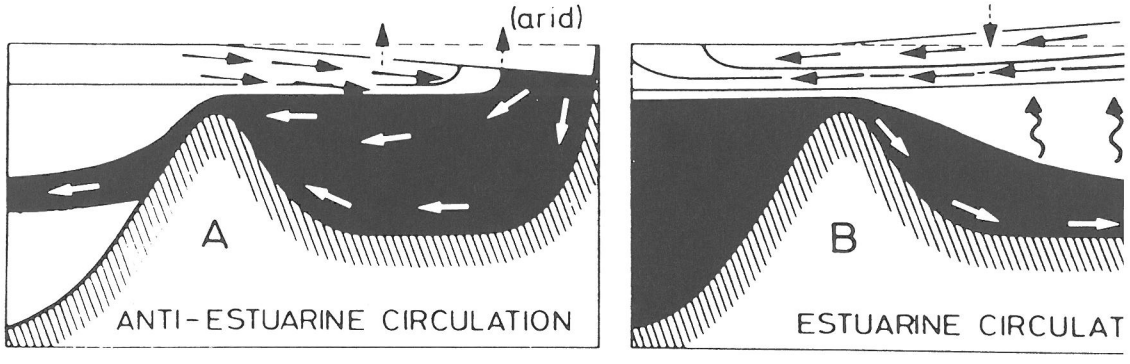
A major division takes place in the middle of the North Atlantic resulting in the Azores Current flowing south-eastward (GOULD 1985). Later divisions are the south-eastward bound (Portugal) Canary Current and the Irminger Current flowing towards the north-west. The former two currents are part of the North Atlantic Subtropical Gyre while the stronger western branch of latter forms the characteristic Polar Front together with the cold and less saline waters of the south-westward going East Greenland Current off south-east Greenland. A weak and variable eastern branch of the Irminger Current flows coast-near around North-West Iceland influencing the North Icelandic coastal waters in an interference with cold and less saline East Iceland Current waters especially in years with appreciable polar influence (Fig. 15) (STEFÁNSSON 1962, 1969; STEFÁNSSON and GUÐMUNDSSON 1969; MALMBERG 1985, 1986; MALMBERG and KRISTMANNSSON 1992).

Parts of the NAD overflow the European shelf as *e.g.* in the Bay of Biscay, the Irish Sea, the English Channel, and the North Sea (Fig. 15) (DIETRICH 1970; DIETRICH et al. 1975; PINGREE and GRIFFITHS 1978; PINGREE and LE CANN 1990; PINGREE 1978, 1993).
KOUTSIKOPOULOS and LE CANN (1996) reviewed the complex hydrographical situation within the Bay of Biscay. There is a relative weak general anticyclonic oceanic circulation in the centre of the Bay, a seasonally variable and differentiated Biscayan Slope Current (BSC) along the shelf-break (Fig. 15), frequent cyclonic and anticyclonic slope water oceanic eddies ("swoddies"), and residual currents above the French shelf, governed by wind, various eddies, water density and tides. From late spring to early autumn the southern coastal waters (off Galicia, Asturias, and Cantabria) are characterised by upwelling (see upwelling paragraph below) persisting through the period of thermal stratification and very warm waters in the south-eastern corner of the bay (see Fig. 30). In summer and early autumn interactions between tides and the bottom topography are responsible for seasonal tidal thermal fronts above the French continental shelf especially west of Brittany. From spring until autumn there are persisting cold water masses ("bourrlet froid") strongly influencing the outer French shelf and stretching from the Gironde estuary to the English Channel entrance. In autumn a warm water tongue ("langue d'eau chaude") appears close to the Aquitaine coast. In winter there occurs an anomalous situation above the inner French shelf: a thermal inversion with colder fresher waters (mostly runoff from the rivers Adour, Gironde, and Loire) in the surface layer, in intensity increasing towards the north. The Biscayan Slope current is running as a warm coastal winter current along the Portuguese coast and reaches as far as the south-eastern corner of the Bay of Biscay leading to another anomalous situation causing the highest surface water temperatures of the year along the northern Spanish coast in the winter

months of January and February. Along the northern Biscayan and Celtic shelf-break the slope current is strongest in late summer without an outstanding thermal effect (PINGREE and LE CANN 1990; KOUTSIKOPOULOS and LE CANN 1996).

There are also currents in the deep-sea. GAGE (1997) described effects of tidal bottom currents in the lower end of the Setúbal Canyon. Off the Porcupine Seabight at depths of 4009 m and between 2000 m and 4700 m in the Bay of Biscay deep tidal currents have been described as having marked influence on the behaviour of predatory demersal fishes (GUENNEGAN and RANNOU 1979; MERRET and HAEDRICH 1997) and partly on deposition of phytodetritus (BILLET et al. 1983). In archibenthal and bathyal depths there are various types of downslope and alongslope currents depending on the slope angle and local hydrographic situation shaping the surface structure and sedimentology of the area on different orders of magnitude (Chap. 3.1). TYLER (1988) cited four different patterns related to some seasonality in the Rockall Trough: a summer-autumn maximum in the Norwegian Sea Deep Water overflow; an autumn minimum in the upper ocean circulation around the Rockall Bank; an autumn-winter maximum in the strength and breath of the European continental slope current; and a winter-spring maximum in eddy kinetic energy in the open waters and over the full depth range of the Rockall Trough. Above that seem oceanic large-scale hydrodynamic patterns to influence deep-sea currents in various patterns. These different types and strengths of currents in the deep-sea are considered to contribute to habitat heterogenity and thus deep-sea biodiversity (GAGE and TYLER 1991; GAGE 1997).

The NAD enters the Norwegian Sea mainly through the Faeroe-Shetland Channel after which a branch diverts into the North Sea. The Norwegian Current deriving from the NAD transports warm (4°-12°C) and saline (34.8-35.2 ‰) Atlantic water along the Norwegian continental shelf. Off the northern Norwegian coast the current splits in two branches, one continuing along the continental slope as the West Spitzbergen Current. West of Svalbard/Spitzbergen Atlantic waters are cooling and submerging and form a subsurface current in the Arctic Ocean along the continental slope towards the east extending from about 200-900 m depth, below which is the Arctic deep water. The other branch is diverting into the Barents Sea as the North Cape Current or later called Murman Coastal Current (Fig. 15) .
The Atlantic water is isolated from the Norwegian coast by the Norwegian Coastal Current, which is a continuation of the brackish Baltic Current fused with North Sea water and freshwater runoff flowing out of the fjords (Fig. 18). This less saline coastal current water spreads out in a wedge-shaped form above the heavier Atlantic water in seasonal variations. Towards the north both currents merge resulting in a salinity increase near the coast (Fig. 15) (ANGEL 1979b; BLINDHEIM and LOENG 1981; MEINCKE 1983; BRATTEGARD and HOLTHE 1995).



Figs. 17 (A), 18 (B): Anti-estuarine and estuarine circulation in basins with excess evaporation and with excess precipitation respectively (from SEIBOLD and BERGER 1993). The estuarine basin (A) is characterised by downwelling, hence low fertility and high oxygen content. The estuarine basin (B) is characterised by upwelling and salinity stratification, hence high fertility and low oxygen content. Fig. 18 (B) depicts the situation of the Baltic Sea circulation and of many Norwegian fjords in a cross-section (compare BRATTEGARD and HOLTHE 1995). The contrary situation of Fig. 17 (A) corresponds to the Mediterranean Sea where an under-outflow of warm saline waters above the Gibraltar sill is spreading in the East Atlantic forming a distinct layer at ~ 1000 m depth (compare Figs. 23-27).

The Greenland-Iceland-Faeroe-Scotland Rise prevents deep Atlantic water entering the Norwegian and Greenland Seas and hence the Arctic Ocean. Warm and saline Atlantic surface waters flowing above this hydrological barrier system and further through the Nordic Seas into the Arctic Ocean are separated by cooling and freezing into ice, shallow fresher waters, and saline deep waters which sink.
Besides eastward going currents along the Siberian coast which take up the Siberian river freshwater runoff, there are current motions around the anticyclonic Beaufort Gyre centred over the Canadian Basin and the Transpolar Drift with the main surface outflow being the East Greenland current carrying southward about 10 % of the multiyear pack ice from the Arctic Ocean and icebergs from East Greenland glaciers (Fig. 19).
The Arctic Ocean - largely surrounded by land masses as being a mediterranean sea - is linked to the world ocean by the Bering Strait (with a sill of only ≤ 45 m depth), the Fram Strait between NE-Greenland and Spitzbergen and minor passages to the Barents Sea. Approximately 80% of the Arctic basin water exchange takes place through Fram Strait while the Bering Strait inflow passes mainly through the Canadian Arctic–West-Greenland waterways into the NW-Atlantic (Zenkevitch 1963; Vinogradov 1968; Bramwell 1977; Angel 1979b; Meincke 1983; Dunbar 1985; Bearman 1989; Bleakley and Alexander 1995).

The East Greenland Current waters are less saline (31-34 ‰) and colder (-1.5 to +2°C) (Einsele 1992) than NEA waters derived from the subtropical NAD. Thus markedly oceanic fronts with sharp physicochemical gradients and strong hydrodynamics develop where the two water masses meet (Dietrich 1964; Wadhams 1979) or where mid-gyre convection occurs in the Norwegian-Greenland Sea (Aagaard et al. 1985; Sarnthein and Altenbach 1995) (Figs. 15, 31). The East Greenland Current flows mainly along the Greenland continental slope north of the Greenland-Island Rise, while it enters the SE-Greenland shelf south of the deep channel of Denmark Strait and where the western branch of the Irminger Current is found off the SE-Greenland slope with the Polar Front in-between (Fig. 15) (Malmberg 1985).
The Jan Mayen and East Iceland Currents are branches of the East Greenland Current diverting into the Greenland Sea north respectively south of Jan Mayen

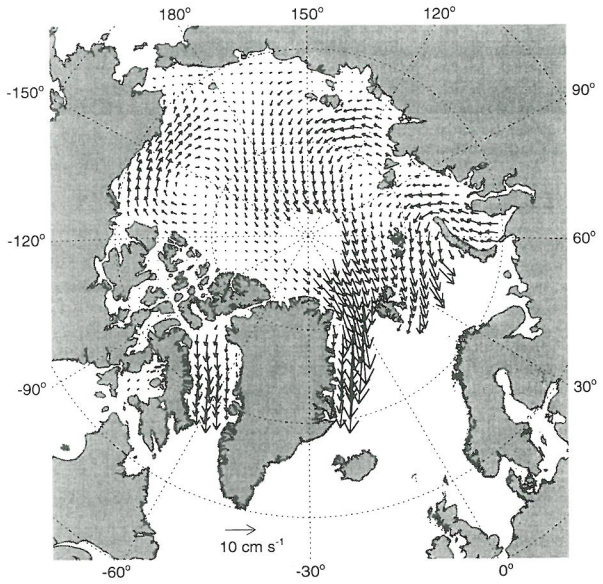


Fig. 19: Average ice field velocity – winters 1987/88 and 1994/95 (from Kreyscher 1998).

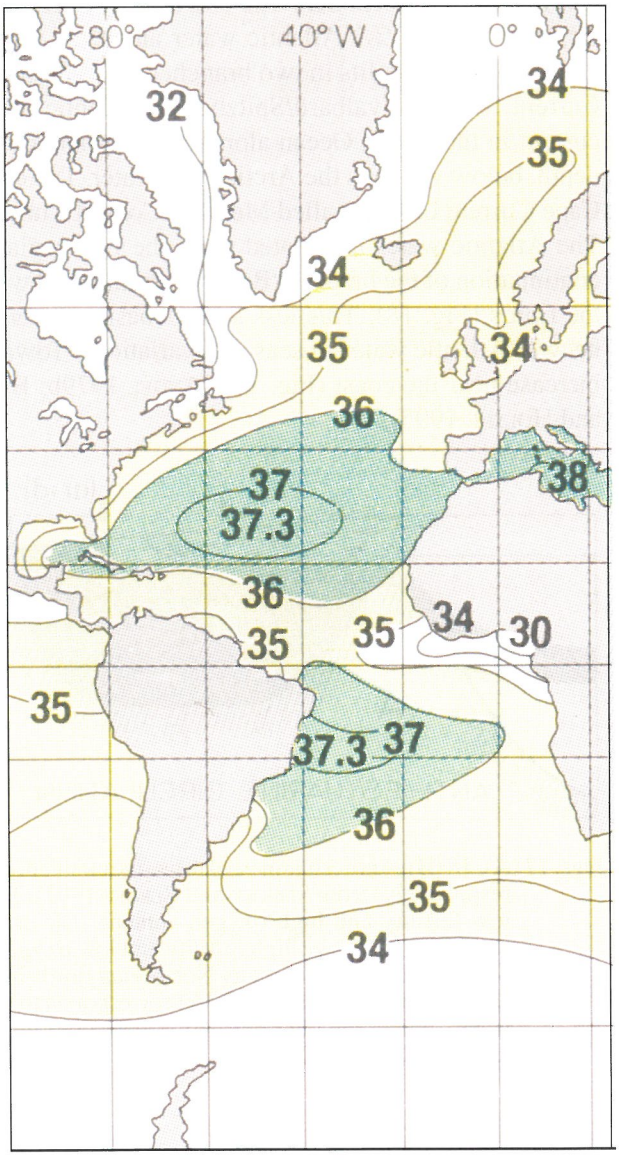
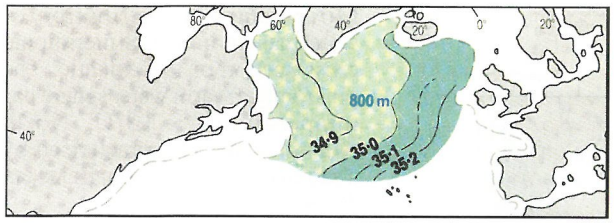
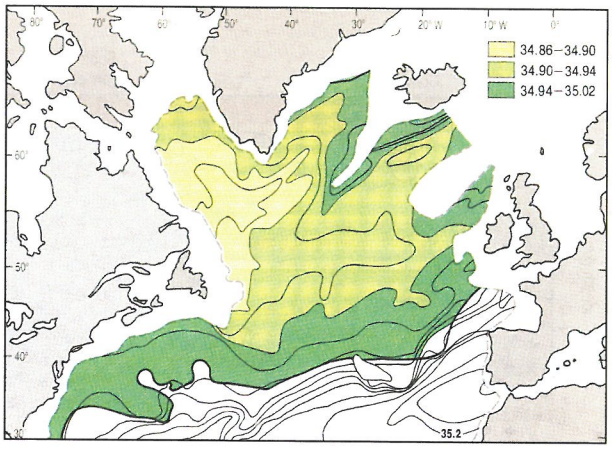
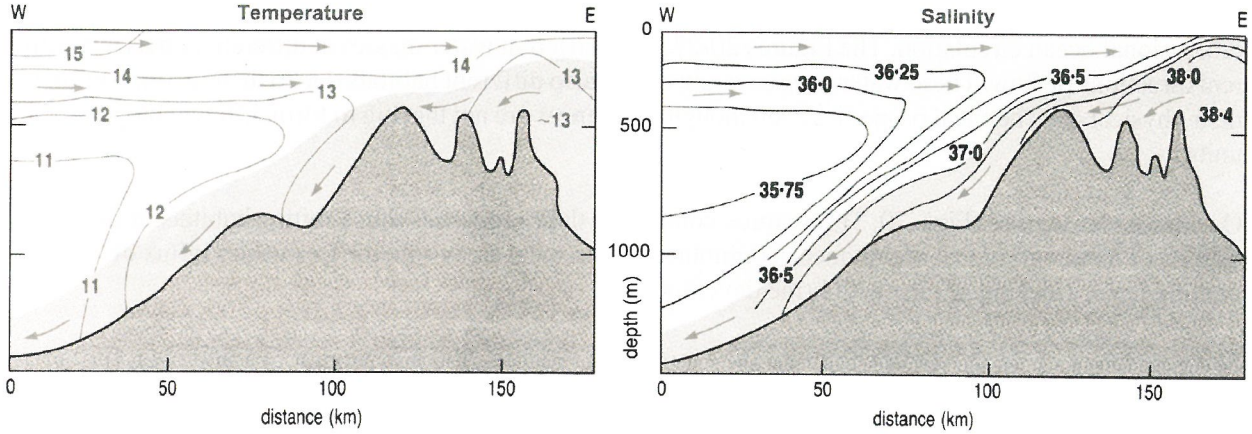


Fig. 20: Mean annual distribution of surface salinity in the Atlantic (from Bearman 1989).

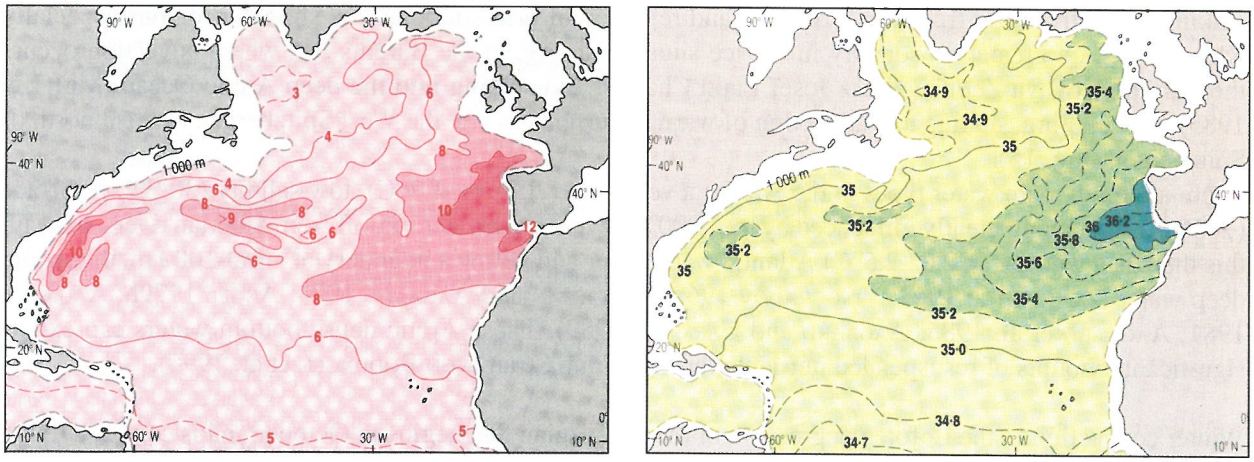




Figs. 21, 22: Spreading and slow mixing of Western Atlantic Subarctic/Labrador Sea Water at 500-900 m depth (above) and at ~ 1500 m depth (right) characterised by changes in salinity (from BEARMAN 1989).



Figs. 23, 24: W-E section across the Gibraltar sill showing the surface inflow of less saline Atlantic waters and the outflow of Mediterranean water of higher salinity at depth (from BEARMAN 1989).



Figs. 25, 26: Distribution of temperature (left) and salinity (right) at ~1000 m depth in the North Atlantic showing the spread of Mediterranean Water (from BEARMAN 1989).

where they take part in the formation of cyclonic gyres (Fig. 15) (AARGAARD et al. 1985; BOURKE et al. 1987; BLINDHEIM 1989).

The relative cold, low salinity waters of the East Iceland Current characterise the northern slope of the Iceland-Faeroe Rise from NE-Iceland towards the Faeroes and spreads at subsurface/intermediate depths towards the Norwegian continental slope, intruding between warm more saline Atlantic water deriving from the NAD and Norwegian Sea deep water (BLINDHEIM and LOENG 1981).

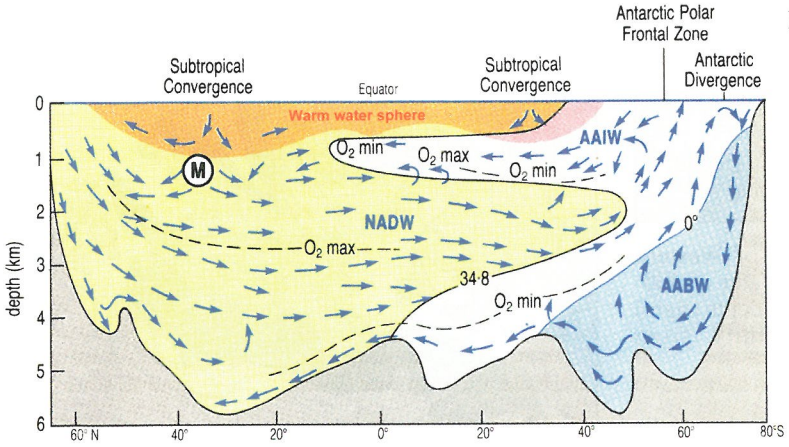


Fig. 27: Movement and distribution of watermasses in a N-S meridional cross-section of the Atlantic. The pink/orange warm water sphere has temperatures > 10°C; North Atlantic water is characterised by a salinity > 34.8 ‰ (from BEARMAN 1989).

NADW = North Atlantic Deep Water
M = deep inflow of Mediterranean Water at latitude 36°N
AAIW = Antarctic Intermediate Water
AABW = Antarctic Bottom Water, < 0°C

Water masses can be distinguished by their conservative properties temperature and salinity within the three-dimensional ocean circulation. The Figures 20-27 show different water masses at different depths with different directions of flow. These water masses might depict also different habitats due to their distinct origin and their physical and chemical properties even though differences are not that big to form different biogeographic units.

Oceanic water masses (Figs. 20, 31) are quite constant in their properties thus limiting habitats of fluctuating salinity of biogeographical importance geographically to coastal areas with the freshwater influx of estuaries, melting ice or freezing sea ice with brine development.

Surface waters of the NAD flowing into the North-East Atlantic, the Norwegian Sea and even further are exceptionally warm and saline for these latitudes, with temperature and salinity values in excess of 8°C and 35.25 ‰ (Figs. 15, 20, 34, 35).
Besides surface circulation (Chap. 3.3) there are complex patterns of deep circulation with Antarctic Bottom Water (AABW) flowing as far as 40° Northern latitude (Fig. 27). The North Atlantic Deep Water (NADW) lying above is derived from different sources: Dense Arctic bottom waters are formed through cooling and sinking respectively by freezing, formation and rejection of brine in polar and subpolar regions especially where there is a greater seasonality in the ice situation as *e.g.* in the Barents Sea where advection occurs through the Novaya Zemlya-Franz Josef Land Channel and sinking into the deep Arctic Ocean (MIDTTUN 1985) or of cooling, sinking and advection of warmer currents as *e.g.* the West Spitzbergen Current north of Spitzbergen (Fig. 15).
There are three main water types in the Arctic: a very cold (-1.5° to -1.7°C), low salinity (30-32‰) surface (±150 m) layer being greatly influenced by the 3000 km³/year freshwater run-off from Siberian rivers, beneath this there is a warmer (< 2.0°-2.5°C) Atlantic water layer and below a boundary at ~750-1000 m, the Arctic deep water (ZENKEVITCH 1963; VINOGRADOV 1968; COACHMAN and AAGAARD 1974; ANGEL 1979b; AAGAARD 1981; AAGAARD et al. 1985; AAGAARD and CARMACK 1989). These Arctic dense bottom waters can export significant amounts of resuspended nutrients through Fram Strait (VON BODUNGEN et al. 1995).

Winter convection in the Lofoten depression of the Norwegian Sea begins in October and is confined to the first zone above the thermocline (0-50 m), but affecting all waters down to at least 2000 m in February, and the begin of thermal stratification in April which causes a gradual rise of temperature in the layer from 600-800 m to the surface (VINOGRADOV 1968).
Downwelling water masses by mid-gyre convection form deep and intermediate waters in the Norwegian-Greenland Seas, called Norwegian Sea respectively Greenland Sea Deep or Intermediate Water (NSDW/GSDW), sometimes also called Arctic Bottom Water (ABW). These very cold water masses spread south through the Denmark Strait deep channel (sill depth ≥ 600 m) or spill intermittently over the Iceland-Faeroe Rise with a saddle depth of ~ 500 m, or through the Faeroe Bank Channel with a saddle depth of ≤ 850 m into the Atlantic, where they form the core of the NADW (Figs. 27, 28). Below warm and more saline Atlantic waters there are NSDW masses which flow through the Faeroe Bank Channel bathing the southern slope of

the Iceland-Faeroe Rise at depths exceeding ~800 m. (Stefánsson 1962, 1969; Stefánsson and Guðmundsson 1969; Westerberg 1979; Swift et al. 1980; Meincke 1983; Swift et al. 1983; Aagaard et al. 1985; Malmberg 1985, 1986; Bourke et al. 1987; Blindheim 1990; Hansen et al. 1990; Malmberg and Kristmannsson 1992; Reinert 1995; Sarnthein and Altenbach 1995;). The Norwegian-Greenland Sea is believed to be one of the most important regions of the world oceans in the formation of deep water for the global salinity conveyor belt (Richter 1992; Henrich et al. 1995).

Additional components of the NADW derive from downwelling parts of the North Atlantic Drift south of the Greenland-Iceland-Faeroe-Scotland Ridge, and intermediate waters of distinct characteristics as the Mediterranean Water (temperature 12-6°C, salinity 36.2-35.2 ‰) (Figs. 23-26) and Western Subarctic/Labrador Water (temperature 3-4°C, salinity < 34.92 ‰) (Figs. 21, 22). The Mediterranean water flows out of as subsurface compensation to surface inflow at depths above the sills of the Strait of Gibraltar. From there is spreads out at intermediate depths in the eastern North Atlantic (Figs. 17, 23-26). (Sverdrup et al. 1942; Dunbar 1951; Neumann 1968; Dietrich 1963, 1964, 1970; Coachman and Aagaard 1974; Dietrich et al. 1975; Swift et al. 1980; Aagaard 1981; Swift et al. 1983; van der Spoel and Heyman 1983; Swift 1986; Bearman 1989; Broeker and Denton 1989; Thiede et al. 1989; Einsele 1992; Sarnthein et al. 1994). At intermediate depth there is a northward along-slope current along the Celtic and Scottish continental slope associated with the Mediterranean water masses (Figs. 25, 26, 28) (Ellett et al. 1980; Booth and Ellett 1983).

At some parts of the NEA *e.g.* the Denmark Strait; the Barents Sea, the Faeroe Bank area, or the Rockall Trough (Fig. 28), different water masses form a complex vertical situation. In the latter case there is cold water with low salinity of Labrador origin filling the bottom of the Rockall Trough with some intrusions of extremely cold and even lower saline waters of Norwegian Sea origin. These waters are situated beneath a layer of warmer Mediterranean water of higher salinity, spread between 800 and 1200 m depth and with up to 200 m vertical extension, which again is located below the mixed Atlantic waters (Rätz 1984; Mauchline 1990).

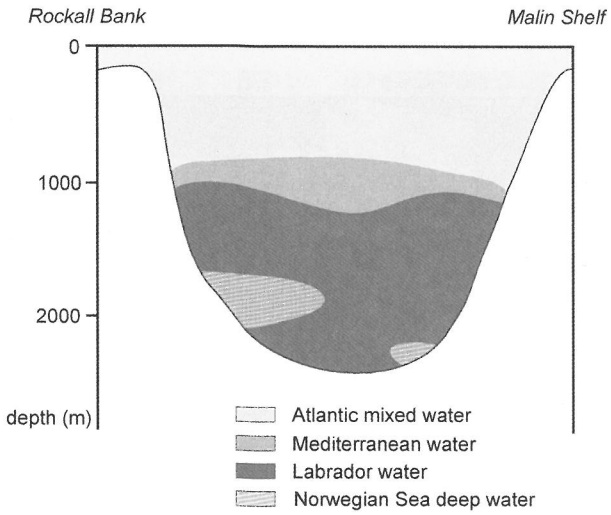


Fig. 28: Cross-section of the Rockall Trough showing water masses of different origin (redrawn after Rätz 1984).

Due to the hydrological isolation in past geological periods (Chap. 3.1) and warmer (marine) climates (Chap. 3.4) there might have been stagnant low oxygenated water masses in the Arctic and Norwegian-Greenland basins (Thiede et al. 1990). The flow of NAD Atlantic water masses into the northern seas and resulting oxygen-rich deep-water formation as described above only occurred during the last 13,000 years with fluctuations in the NAD through late Pleistocene/early Holocene climate variations.

Upwelling occurs *i.a.* at locations with current divergences (oceanic equatorial upwelling, not in the OSPAR area) and might also occur where subsurface currents are deflected by bottom topography on a local scale, and under the influence of winds causing off-shore movement of waters (coastal upwelling) (Bearman 1989). Surface waters get replaced by waters from below which are often nutrient rich thus considerably enhancing surface productivity. Strong localised offshore flows are typically associated with elongate bodies of surface water "filaments" that differ from their surroundings (Merret and Haedrich 1997). While the enhanced abundance of primary producers is carried further offshore in periods of intensive upwelling, herbivorous communities are carried from eutrophic to oligotrophic waters passing through certain stages of succession at the same time (Vinogradov 1997). Communities in upwelling regions may be rich in biomass but are always poor in species (Zezina 1997) and may lead to increased concentrations of foraging fish and seabirds (Gubbay 1999).

In the OSPAR area upwelling might take place at ice edges (Dunbar 1985) and at eastern boundary currents in response of the influence of NE-trade winds (Bearman 1989; Mittelstaedt 1991; Van Camp et al. 1991). The most striking location of upwelling within the OSPAR area is at Galicia/NW-Spain and Portugal off the Iberian peninsula and is separated from the NW-African upwelling by the Gulf of Cadiz and the entrance to the Mediterranean with its peculiar hydrographic situation (Figs. 17, 23, 24, 29, 30). Upwelling of cool and nutrient rich waters off west and north-west Iberia starts in June close to the coast, is best developed from late July to September by which time it may extend to 200 km offshore with surface cooling effects even reaching as far out as 600 km, and may last till October (Wooster et al. 1976; Fraga 1981; Fiúza et al. 1982; Fiúza 1983; Varela 1992; Bode et al. 1996). Bode et al. (1996) showed local variations within the north Iberian upwelling system while Wooster et al. (1976) and Fiúza et al. (1982) identified a peak in surface temperature deficits off Lisbon and Sines, south-western Portugal. Sporadic less intensive upwelling might occur there in winter induced by local northerly winds. Thus production within the Iberian upwelling system is highest on the western coast off the southern half of Portugal (Wyatt and Perez-Gandaras 1989). According to Fiúza (1983) this is related to the topography of the south-western Portuguese shelf which is fairly narrow with a very steep slope and several submarine canyons (Chap. 3.2), providing a steep three-dimensional upwelling pattern. Thus thermal gradients are closer to the coast combined with southward increasing seasonal Trade wind influence. The northern Portuguese coastal shelf is flater and widens towards the north with a fairly two-dimensional upwelling with isotherms being parallel to the bottom topography. The southern Algarve coast if affected directly by upwelling only under infrequent local winds but occasionally indirectly by cool upwelled waters turning around Cabo São Vincente from the west coast (Fiúza 1983).

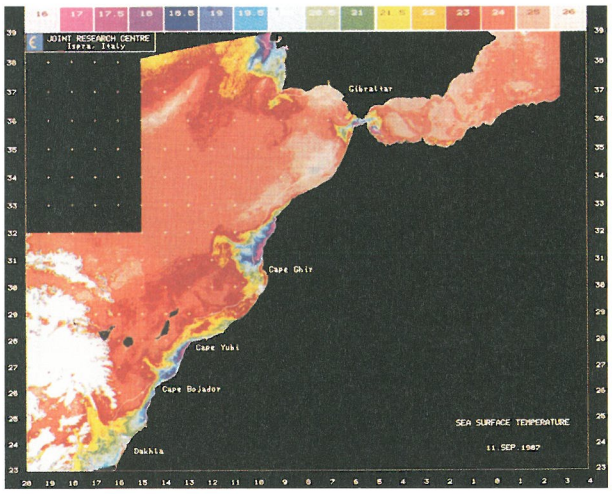


Fig. 29: Sea surface temperatures (SST) of NW-Africa and the southern Iberian peninsula on the 11.9.1987, derived from IR-satellite images. Concerning the OSPAR area it shows a differentiation of marine climates SW of the Iberian peninsula, *i.a.* areas of upwelling (blue) off Portugal (from Van Camp et al. 1991).

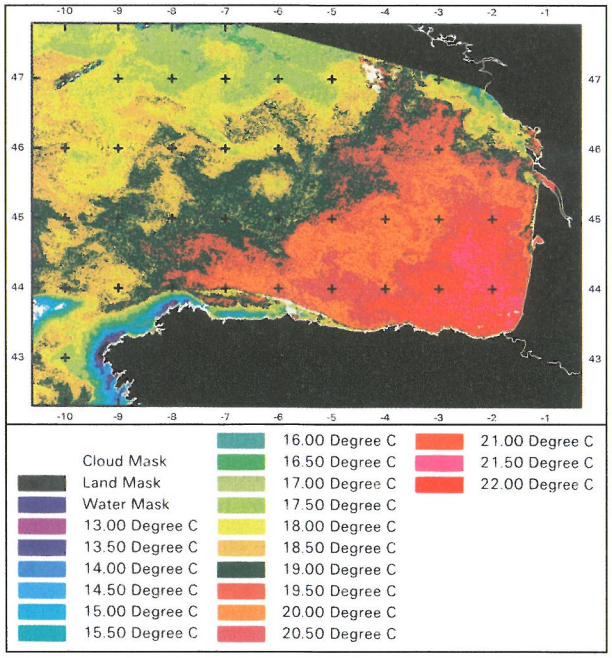


Fig. 30: Sea surface temperatures of the southern Bay of Biscay and Galicia coasts on the 6.8.1998 derived from IR-satellite images showing a differentiation of marine climates, *i.a.* areas of upwelling (blue) (from IEO-Santander 1998).

There are seasonal changes with the warm winterly poleward long-shore Biscayan slope Current (Fig. 15) intermingling with the cool summery upwelling regime in spring and autumn (Frouin et al. 1990; Koutsikopoulos and Le Cann 1996). Besides upwelling there might occur downwelling phases enhancing sedimentation of produced biomass out of the euphotic zone (Bode et al. 1996). Below upwelling areas there can develop hypoxic reducing zones due to remineralization processes of enhanced detritus masses (Chap. 3.1).

Due to episodical changes in atmospheric climates coastal upwellings are liable to fluctuations which might cause severe implications on biological patterns and human economy (FIÚZA et al. 1982; SHERMAN 1992; WYATT and LARRAÑETA 1988; WYATT and PEREZ-GANDARAS 1989), while ≥ 50% of the world commercial fish catches depend on this feature which covers only 0.1% of the world ocean surface (FAO 1972; COX and MOORE 2000).

Large scale horizontal water movements can play an important role in the dispersal of species (*e.g.* VAN DER SPOEL and HEYMAN 1983; ANGEL 1993). Fronts depict horizontal and vertical boundaries between different water masses and can occur at all scales of time and space *i.a.* as estuarine fronts, tidal fronts, coastal turbidity fronts, shelf-break fronts, and oceanic fronts. Thus fronts can serve *i.a.* as distribution barriers, mixing zones, concentration zones, nursery areas, areas of taxonomic and ontogenetic selection, areas of enhanced production, areas of initiation of succession, areas of vertical export, areas of horizontal transport, areas of temperature and salinity anomalies, as ecotones, and as entire ecosystems (NEUMANN 1968; SOURNIA 1994). Frontal regions are often transition areas between well mixed, cold waters and stratified, warmer waters. Mixed water means high nutrients but poor light conditions; stratified water means good light conditions but limited nutrients. The frontal zone is a region of high production due to the compromise between adequate light and adequate nutrients (NEUMANN 1968). Even less understood in their effect on biogeography are along-front flows which are associated with all types of fronts (SOURNIA 1994).
The major oceanic fronts in the OSPAR area are the Polar Front, the Arctic Front, the Subarctic Front, and marginal the Azores Front.
The Polar Front runs between the very cold Polar Waters of the East Greenland Current and modified Arctic waters in the Greenland Basin, modified North Atlantic Water (Irminger Gyre/Iceland Basin), and Subarctic Water (Labrador Basin). It is far less pronounced north of Iceland because of the partly similar character of the Arctic Waters and the existence of eddies along the front indicating its possible instability (WADHAMS et al. 1979).
The Arctic Front is situated between the Arctic Water of the Greenland Basin, Arctic Waters of the northern Barents Sea, and the North Atlantic Water of the Norwegian Current and its descendants. The Subarctic Front lies between the Subarctic Water of the Labrador Basin, the modified North Atlantic Water of the Irminger Gyre/Iceland Basin, and the North Atlantic Central Water (SOURNIA 1994) (Figs. 15, 31). Interestingly the distribution of the Greenland halibut (*Reinhardtius hippoglossoides*) in deep waters of the North Atlantic and Norwegian-Greenland and Barents Seas reflects the position of Polar and Arctic fronts (TROYANOVSKY and LISOVSKY 1995).
The meandering Azores frontal system lies south of the Azores archipelago just south of the OSPAR boundary above the MAR and separates Western Atlantic Water from Eastern Atlantic Water. The former is poorer in nutrients resulting in only 50-60% of the chlorophyll level of the Eastern Atlantic Water and is thus also poorer in zooplankton (decapod) abundance (DOMANSKI 1986; GOULD 1985).

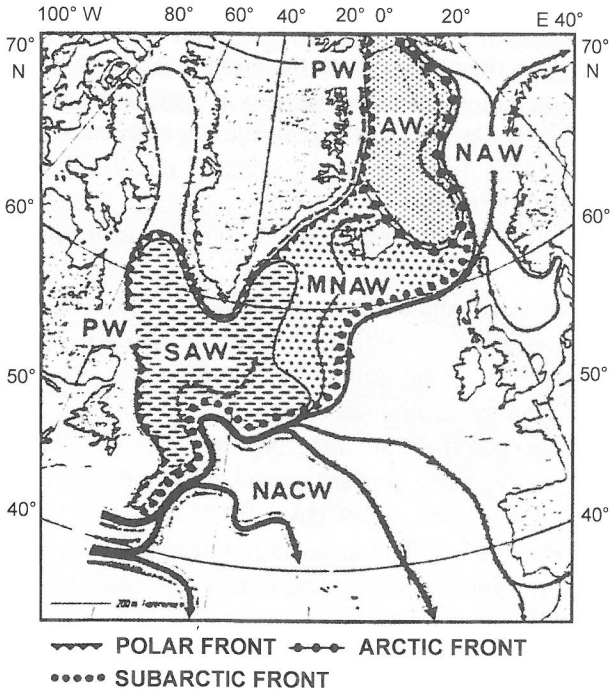


Fig. 31: Upper-ocean water masses and fronts in the North Atlantic (from DICKSON et al. 1988).
PW: Polar Waters
AW: Arctic Waters
SAW: Subarctic Waters
NAW: North Atlantic Waters
NACW: North Atlantic Central Water
MNAW: Modified North Atlantic Water

When parts of oceanic currents and water masses (*e.g.* NAD and descendants) are approaching the European shelf (*e.g.* in the Bay of Biscay, the Irish Sea, the English Channel, and the North Sea) intermediate deep along-shore currents can form (MERRET and HAEDRICH 1997) and shelf-break fronts develop

frequently were thermally stratified and unstratified waters meet. Turbidity fronts occur almost along all coasts at some depth less than 50 m. Front development on the shelf is related to seasonally stratification of certain nutrient poorer water masses in summer that form fronts with mixed water masses richer in nutrients. Tidal occurrence and velocity in combination with (bottom) topography determines duration and location of mixed waters and frontal positions. Light penetration and nutrient availability are the determining parameters that influence phytoplankton growth and the following food web related to enhanced primary production to congregate in the vicinity of fronts. Even benthic life might be influenced at locations with restricted flushing of bottom waters due to development of stratification and fronts. At such locations winter water might persist for much of the spring and summer as a dome of cold water overlying the seabed. On the other hand localised enrichment of bottom communities has also been described to occur below frontal zones. There are markedly shelf-break and tidal front systems all around the shelves in the OSPAR area with implications for the biology, *e.g.* shelf-break fronts are frequently separating oceanic and neritic pelagic species. (*e.g.* CRISP and SOUTHWARD 1953; SOUTHWARD and CRISP 1954; LEE 1970; PINGREE et al. 1974; PINGREE et al. 1975; PINGREE et al. 1976; SIMPSON et al. 1977; PINGREE and GRIFFITHS 1978; SIMPSON et al. 1978; HOLLIGAN 1978, 1981; LEE and RAMSTER 1981; OWEN 1981; SIMPSON 1981; BEARDALL et al. 1982; REES and HOPE-JONES 1982; EARLL and FASHAM 1983; HOLME and REES 1986; PINGREE and LE CANN 1990; PINGREE 1978, 1993; ANGEL 1993; DICKEY-COLLAS et al. 1996; KOUTSIKOPOULOS and LE CANN 1996; BEGG and REID 1997; LONGHURST 1998).

3.4 Energy balance and marine climates

Differences in salinity, nutrients, oxygen, light duration and penetration, habitat diversity, ..., can influence biogeographic patterns in local situations, but temperature, characterising water masses to a large extent, has the most important effect on biological distribution patterns on the oceanic or global scale (*e.g.* HEDGPETH 1957; KINNE 1970; VAN DEN HOEK 1975; MICHANEK 1979; EARLL and FARNHAM 1983; GLÉMAREC 1973, 1988; BRIGGS 1974, 1995; LONGHURST 1998).

Marine climates have undergone several severe changes over geological time (Fig. 32). Realising that the Atlantic developed from the Jurassic/Cretaceous on (Chap. 3.1) it is obvious that there have been major changes in marine biocoenoses as well (*e.g.* MENZIES et al. 1973; VAN DEN HOEK 1975; BRIGGS 1970, 1974, 1987; HENRICH et al.1995; SARNTHEIN and ALTENBACH 1995). Ancient thermohaline circulation patterns have resulted in different marine climates due to different geographical constellations and different regional and local currents as described in the chapters 3.1 and 3.3. Therefore biological patterns depending on temperature and nutrients etc. related to currents and water masses have changed as well.

To the south and to the north of the tropical Tethys – which occupied a belt between ~50°S and ~50°N – were warm temperate realms while the temperature at the poles fluctuated between +10° and +16°C during the Cretaceous. Polar temperatures only dropped to a point at which the development of cold temperate floras could have been initiated only at the beginning of the Tertiary, with winter surface temperatures of 5-8°C at Spitzbergen from this time onward (VAN DEN HOEK 1975).
During the early Tertiary period, especially the upper Eocene, there was a tropical to subtropical climate in the NEA and the Arctic (EKMAN 1953; BOWEN 1966). The establishment of a circum-Antarctic circulation in the Eocene led to a temperature fall in both the southern ocean and the northern hemisphere (GOLIKOV et al. 1990). Global cooling effects near the mid/late Eocene and the early/late Oligocene were probably been responsible for the establishment of cold-temperate conditions at these latitudes according to BRIGGS (1974/ 1995).

VERMEIJ (1992) highlighted the fact that several marine genera and species (several molluscs as well as the limpet, kelp, and lobster genera *Puncturella, Helcion, Laminaria* and *Homarus*) have disjunct distributions in shallow temperate NEA and southern Africa biota but are missing in tropical West Africa. After the final reopening of the Bering Strait ~ 3.5 mio years ago in the Pliocene and the following interchange of cool temperate and polar marine species through the Arctic with a massive dominance of Pacific invaders (at least for molluscs) into the NEA (VERMEIJ 1991, 1992; GLÉMAREC pers. com.), no such species reached southern Africa. This provided evidence that the tropical belt acted as an effective barrier to further southward distribution

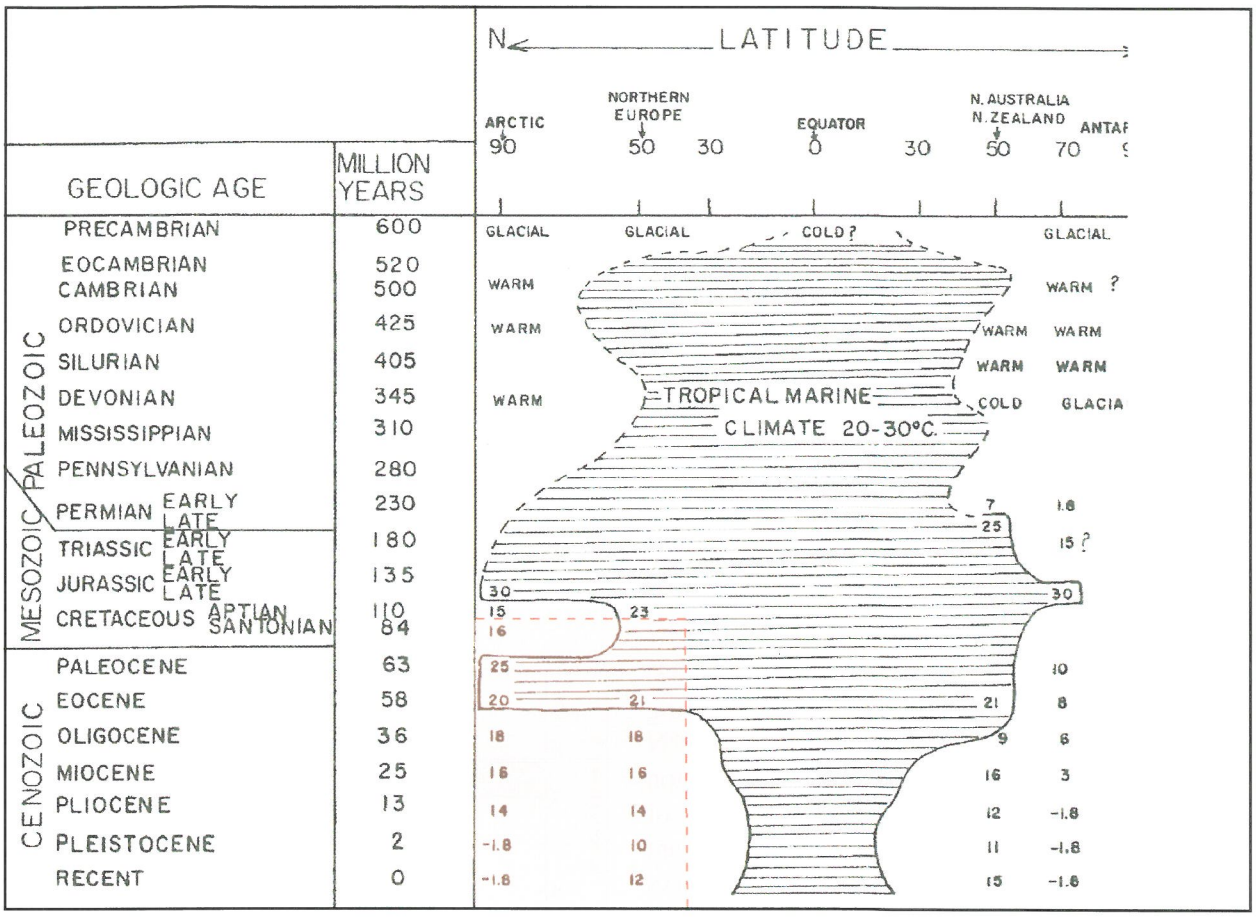


Fig. 32: The evolution of marine surface climates. The OSPAR area is indicated red (from MENZIES et al. 1973; modified).

from Pliocene onward and even during glacial times because dispersal of the main shallow water taxa by equatorial submergence in cold deep waters could not take place. The implications are that the trans-equatorial distribution of shallow temperate water related species was achieved before the late Pliocene rather than during glacial periods (VERMEIJ 1992).

The Arctic Ocean was substantially warmer during the Pliocene than it is today (Fig. 32) so that many species that would be unable to invade from the Pacific into the Atlantic via the Arctic today were able to do so at that time after the reopening of the Bering Strait (VERMEIJ 1991). VERMEIJ (1991) identified 295 mollusc species that derived from the trans-Arctic interchange of which were 261 of Pacific and only 34 of Atlantic-Arctic origin.

Climatic and current (and thus salinity) pattern alternations during the Quaternary period resulted in the abundance of either warm- and cold-water relicts as characteristic features in the Norwegian coastal, Barents, White, and Baltic Seas encountered frequently in small scale habitat areas (ZENKEVITCH 1963; GOLIKOV et al. 1990; BRATTEGARD and HOLTHE 1995).

The Arctic was isolated completely from the Pacific and partly from the Atlantic related to a sea level lowering in the Pleistocene (ZENKEVITCH 1963; GOLIKOV et al. 1990). During the Pleistocene the open Atlantic sea surface temperatures were ~3°C colder during the winter and ~6°C colder than the average annual temperatures. Therefore surface isotherms shifted that much southward that boreal floras and faunas impoverished considerably and cold temperate/boreal species were present in the southern region of the OSPAR area and even entered the Mediterranean Sea (*e.g.* EKMAN 1953; DE LATTIN 1967; FROGET et al. 1972; VAN DEN HOEK 1975; RAFFI et al. 1985; MALATESTA and ZARLENGA 1986; RAFFI 1986; ANGEL 1993). Reflecting possible causes for evolutionary speciation the Pleistocene was largely a time of biotic impoverishment in

northern hemisphere temperate regions rather than of speciation and diversification despite large changes in climate and sea level (VAN DEN HOEK 1975; VERMEIJ 1991). GOLIKOV et al. (1990) proposed that the formation of the Boreal biogeographic region began with falling sea surface temperatures and cold- and cool-temperate water related fauna *e.g.* the peracarid crustaceans, which first appeared in the cold and glaciated times of the Palaeozoic era, and became widely distributed in the Pleistocene epoch.

ANGEL (1979b, 1993) gives examples for marine climate and related biotic changes in the Holocene and mentions the collapse of the Hanseatic League due to a massive decrease in herring stocks during the "Mini Ice Age" and the mass starvation that occurred in the Faeroes in the 17th century when the cod fishery totally failed probably as a result of a fall in sea temperatures. At the same time cod vanished from Norwegian waters and Iceland was entirely surrounded by pack ice in 1695. Also EKMAN (1953) and ZENKEVITCH (1963) described remarkable oceanographical and biological changes in the Arctic and Subarctic seas due to a warming within the first half of the 20th century. For example LOENG (1987), MIDTTUN and LOENG (1987), SKJOLDAL and REY (1989), BLINDHEIM and SKJOLDAL (1993), and ANKER-NILSSEN (1996) described biological effects induced by meso-scale climate variability within the last decades for the Barents Sea, GOLIKOV et al. (1990) for the White Sea, HOVGÅRD and BUCH (1990) for the East-Greenland-Labrador Sea, DICKSON et al. (1988) for the entire northern North Atlantic, and FIÚZA et al. (1982), WYATT and LARRAÑETA (1988), WYATT and PEREZ-GANDARAS (1989), and SHERMAN (1992) for the Iberian coast.

The scheme of the global radiation balance (Fig. 33) shows that the global equilibrium point of incoming and outgoing radiation is presently located at ~40°N on the northern hemisphere. Besides wind circulation systems the oceans with the specific properties of water and their currents (Chap. 3.3) play a significant role in the global energy exchange (*e.g.* BEARMAN 1989). Similar to terrestrial biogeography there are latitudinal belts of biogeographic zones on the global scale principally influenced by patterns of solar radiation (Chap. 3.4) and currents (Chap. 3.3) that distribute characteristics of marine climates into the pelagial and shallow benthal of latitudes under other atmospheric climate regimes (*e.g.* VAN DER SPOEL and HEYMAN 1983; COUPER 1989; BAILEY 1996). Particularly the NAD (Fig. 15) – evolving from the Gulf Stream – supplies an enormous input of energy which lets climatic and biogeographic zones shift far northward in the north-eastern Atlantic. Thus, especially many pelagic biogeographic boundaries fall together with surface isotherms of the oceans (Figs. 34, 35, 104). Some isotherms have been adopted by biogeographers for regional delimitations *e.g.* the Dunbar line (annual average 5°C isotherm) delimiting Boreal and Subarctic regions and the Ortmann line (annual average 15°C isotherm) separating the tropics from the warm-temperate subtropics (Figs. 43, 62).

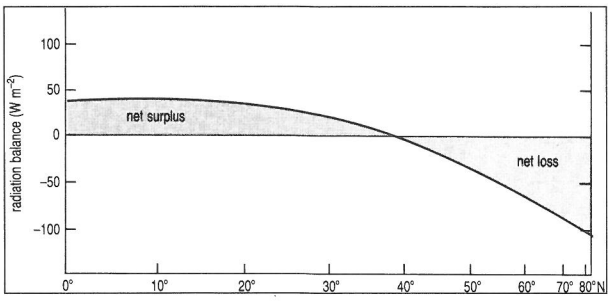
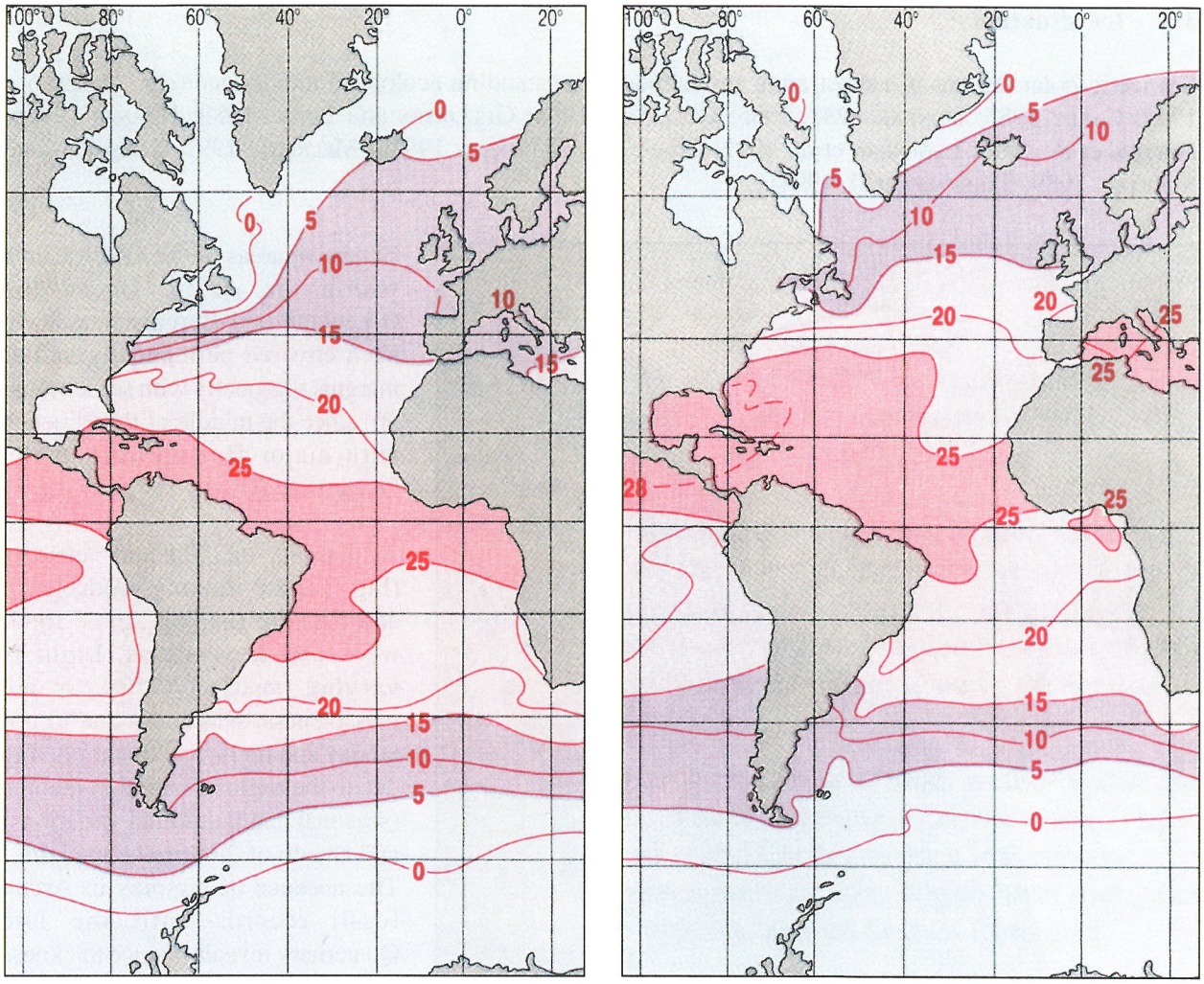


Fig. 33: The radiation balance for the earth-atmosphere system has its point of equilibrium between net surplus and net loss of energy at 40° N (from BEARMAN 1989).

When sunlight hits water, some is reflected depending on the angle of radiation income. Most of the radiation penetrates into the water and 99% of the energy is absorbed in the top 50-100 m in clear water, less in cloudy/ turbid water. Longer waves are absorbed first, with the shorter, higher energy waves penetrating deeper. Depth of light penetration rules the depth of the phytal zone and thus of primary production but also depth and the vertical extension of the mesopelagic twilight layer (Fig. 12, Chap. 3.2) determining diel migrations of most mesopelagic organisms feeding at night in shallow depths and descending during daytime to cooler depths to slow metabolism and to avoid predation by visually orientated predators.

However only surface waters are heated directly by absorbed solar radiation. Any heat that reaches deeper waters must be carried there by slow diffusion or some form of faster convective mixing. Consequently cold deep waters of higher density are situated below warm surface waters thus leading to thermal stratification in regions without vertical convection in the water column. This effect increases with decreasing latitude creating



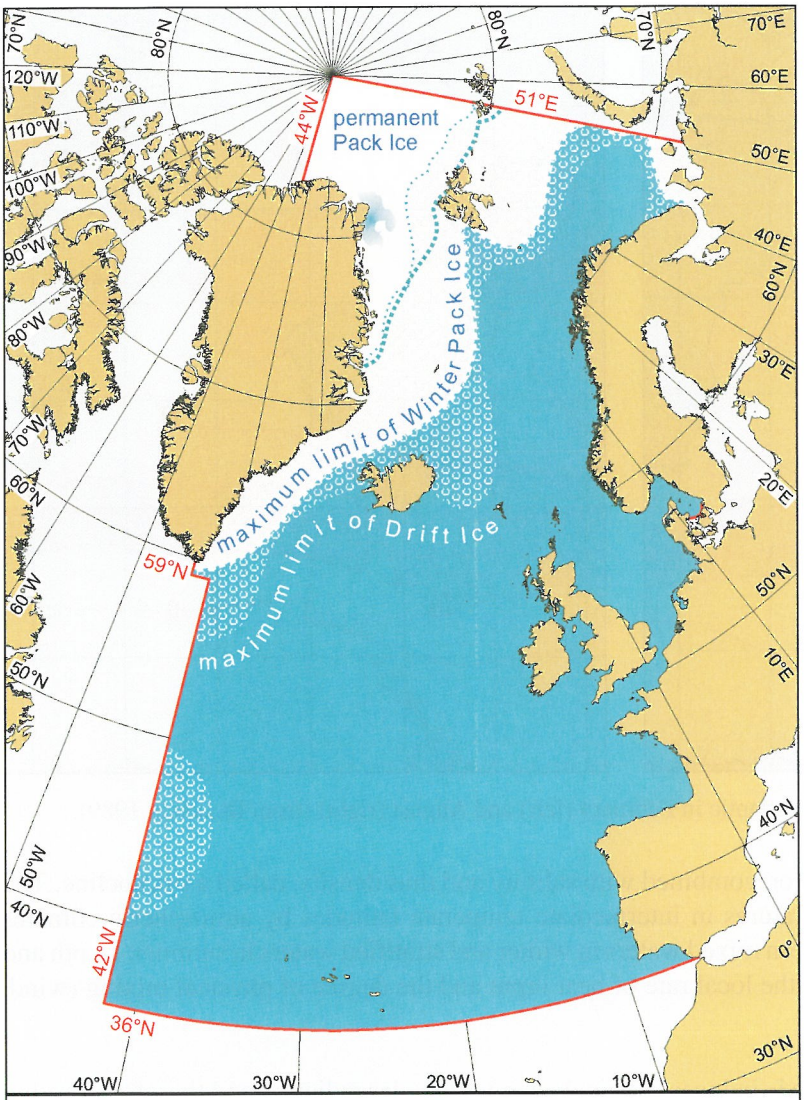
Figs. 34, 35: Surface isotherms (°C) of the Atlantic in February (left) and August (right) (from BEARMAN 1989).

a thin separating layer, the thermocline or, combined with salinity and thus density, called a pycnocline. The seasonal change in sea surface temperatures in intermediate temperate latitudes by atmospheric climates results in a dependent seasonality between mixed waters in winter and stratified waters in summer. Depth and duration of the thermocline depend on the local rate of heat input and the degree of physical mixing (wind, currents, tides and waves).

The inclination of the earth's rotation axis induces seasonal changes of solar radiation and therefore varying atmospheric climates with a strong increase in radiation seasonality towards the poles. The angle of radiation income however is relatively low in Arctic regions even during the polar summer. Therefore the angle of radiation refraction and penetration into the water changes with these seasonal changes due to the physical laws of light fraction at layers of different density.
Light presence with a long insolation duration in the summer and absence in the winter thus has an overwhelming influence on polar primary production and life cycles (HORNER 1982; ALEXANDER 1992; MELNIKOV 1997).
The thermal insulation of less dense very cold (and often less saline) waters at the surface, the albedo of ice-covered regions, and the thermal insulation of the ice-cover itself prevents polar oceans from further vertical freezing.

3.5 Ice situation

Sea ice in polar regions is a substratum and habitat of outstanding ecological importance (*e.g.* Alexander 1992; Carey 1985; Dunbar 1982, 1985; Gulliksen 1984; Gulliksen and Lønne 1989; Horner 1985b; Horner et al. 1992; Legendre et al. 1992; Lønne and Gulliksen 1991b; Melnikov 1997; Sakshaug and Skjoldal 1989; Sakshaug et al. 1994).



NEWP-Northeast Water Polynya
(boundary within open water patches may develop; derived from: GUDMANDSEN et al. 1993, 1994, 1995; HIRCHE and KATTNER 1994; SCHNEIDER and BUDÉUS 1994, 1995, 1997)

approx. mean extend of the permanent pack ice

Comment: The boundaries show absolute expansions: minimum of the permanent pack ice and maximum of drift ice.
Mean extensions tend to be less extreme: limits of the permanent pack ice further south and limits of drift ice further north.

Fig. 36: Sea ice extensions and limits (derived from: US NIC-Sea Ice Data Bank; PIK/Rahnsdorf; AWI; GRIDÅ; Vinje 1985; Alexander 1995; Dunbar 1985; Dietrich et al. 1975; Bramwell-atlas of the oceans; Haack-Atlas Weltmeere).

Extensive areas of the OSPAR area within the Arctic Ocean the Greenland and Barents Seas have been covered permanently and at margins seasonally with sea ice (Fig. 36) since the middle of the Pliocene with major fluctuations in the Quaternary (Clark 1971, 1975).

Availability of light and nutrients (Fig. 37) are limiting productivity and thus are shaping Arctic food-webs and ecosystems. Light is varying spatially due to ice massiveness, seasonally due to polar day and night, and quantitatively due to the angle of radiation income (seasonal and latitudinal variations) and albedo of the surface medium. The absence of diatoms in Arctic fossil records until the late Quaternary reveals that ice thickness was too massive for light penetration and primary production (Melnikov 1997).

According to later author the peculiar ecological features of the Arctic sea ice ecosystem were only acquired ~100,000 years ago thus making the ecosystem a relative young formation from the evolutionary point of view. Others believe that this ecosystem could have developed at former ice-edges at lower latitudes when there was a massive ice-cover. With a reduction of sea ice thickness, penetration of solar radiation was promoted and hence the possibility of photosynthesis for diatoms (Melnikov 1997).

The northern boundary of the Arctic macro-phytal is the southern boundary of the permanent pack ice

because light penetration through 1-4 m thickness of sea ice is too low to allow seaweed growth. Thus Arctic coasts have been re-colonised by ~150 species of macroalgae within the last 18,000 years after the summit of Pleistocene glaciation of the northern hemisphere. Abrasion by ice hinders and prevents growth of algae and other sessile benthic organisms in supra- and eulitoral depths in many places and intertidal organisms are therefore often only found in subtidal depths (MENZIES 1975; LÜNING 1985; BLEAKLEY and ALEXANDER 1990).

Sea ice reduces the exchange of energy between water and atmosphere to a few percent of that which would take place otherwise between the open ocean and the atmosphere (BEARMAN 1989). Even though the overall radiation budget throughout the year is not that low in high latitudes there is only a low productivity caused by permanent low temperatures and a long persistence of ice plates and drift ice inhibiting light penetration into the water. Water directly below the ice cover is much more variable in temperature, salinity and density compared to uncovered surface waters and is often stratified. These changes result from local melting processes, brine formation due to freezing processes and freshwater runoff from glaciers and terrestrial origin. Annual brackish water layers from melting processes are situated below sea ice and above seawater and allow only euryhaline and brackish water tolerant species to thrive (LÜNING 1985).

Commonly differentiated types of sea ice are fast ice and pack ice. The former is formed and remains fast to the coast and is attached to the shore, an ice wall, an ice front, and pack ice, while pack ice is any other area of sea ice (WMO 1970).
When seawater freezes, most of the salt is rejected from the ice lattice resulting in a thin boundary layer of very salty water ahead of the advancing interface. Adding more salt on the top of the layer while freezing proceeds there might occur a "constitutional supercooling" caused by the lower temperature in the ice-water interface compared to the one in the underlying layer. This situation creates an upward flux of heat and a downward flux of salt through the boundary layer. Since the exchange velocity of heat is much higher, brine pockets might get entrapped between platelets while ice-growth continues. Brine pockets and channels are subject to further changes of their position and morphology due to different micro- and macro-scale changes going on within the ice-structure (MAYKUT 1985). In contrast to the Antarctic, where most of the growing ice is granular ice of frazil origin, most of the growing Arctic ice is congelion ice of columnar texture (SPINDLER 1990).

Fig. 37: Microalgal production of biogenic carbon in the Arctic Ocean, north of 65° latitude (from LEGENDRE et al. 1992).
Units:
carbon uptake rate (mg C m^{-2} $year^{-1}$)
standing stock (mg C m^{-2})
area (10^{12} m^2)
production (10^{14} g C $year^{-1}$)

Uptake rate (R) or stock (S)	Area	Annual production	Total production
A Water column production in shelf regions			
27 000 (R)	4.9	1.32	
B Water column production in offshore regions			
9 000 (R)	8.2	0.73	
Total water column production (A + B)			2.05
C Production within the sea ice			
10 000 (S)	0.6–7.0	0.06–0.7 (first-year ice)	
600 (R)	5	0.03 (multi-year ice)	0.09–0.73
Total Arctic production (A + B + C)			2.14–2.78

Fig. 38: Examples of first-year ice-algal concentrations associated with blooming conditions (from LEGENDRE et al. 1992).

Environment	Concentration	References
Freeboard (Antarctic sea ice)	11–80 mg Chl *a* m^{-2}	Kottmeier and Sullivan (1990)
		Garrison and Buck (1991)
Interstitial bottom ice (Arctic)	8–23 mg Chl *a* m^{-2}	Alexander et al. (1974)
	8–26 mg Chl *a* m^{-2}	Horner and Schrader (1982)
	19–130 mg Chl *a* m^{-2}	Smith et al. (1987, 1989)
Interstitial bottom ice (Antarctic pack ice)	2-9 mg Chl *a* m^{-2}	Dieckmann et al. (1990)
Ice platelet layer (Antarctic fast ice)	up to 770 mg Chl *a* m^{-2}	Palmisano and Sullivan (1983), Grossi et al. (1987), Arrigo et al. (1990)
Ice-water interface (Arctic)	≤20 mg Chl *a* m^{-2}	Tremblay et al. (1989)
Retreating ice edge (Arctic)	10 mg Chl *a* m^{-3}	Smith et al. (1985)
	27–41 mg Chl *a* m^{-3}	Niebauer et al. (1990)
Retreating ice edge (Antarctic)	up to ≥6 mg Chl *a* m^{-3}	Smith and Nelson (1985)
Under-ice pycnocline (Arctic)	≤1.5 mg Chl *a* m^{-3}	Legendre et al. (1981)

Significant amounts of primary production in ice-covered oceans take place in localised ice-edge phytoplankton blooms and production dynamics appear to be closely related to seasonal melting of sea ice (Hellum 1994). As an important biological substrate, sea ice has been an area of ecological research for more than one and a half centuries (*e.g.* Horner 1985a). During this period many different terms have been created to describe biota and biocoenoses related to polar sea ice covers: "brown ice", "ankatobenthos", "under-ice benthos", "inverted benthos", "cryovegetation", "cryoplankton", "cryophyton", "cryobionta", "cryoseston", "cryopelagic", "thigmotropic", "sympagic", "psychrophilic", "epontic", "under-ice", "cryointerstitial", "cryoepontic", and "ice/sub-ice" faunas and floras (*e.g.* Golikov and Scarlato 1973; Horner 1985b; Horner et al. 1992; Gulliksen and Lønne 1989; Melnikov 1997).
Nowadays there seems to be an agreement to differentiate the ecological groups and subdivisions of sea ice communities according to their location: ice-water interface at the bottom (ice algae layers frozen into the ice; sub-ice algae mats and strands loosely attached), surface (seawater infiltrated ice-snow interface; surface pools), and sea ice interior (interstitium between ice crystals and platelets; brine channels and crack assemblages). Within these major types there are further variations on the base of different algal communities (Hellum 1994; Horner 1985b; Horner et al. 1992). It appears that pack ice communities are dominated by planktonic forms, while fast ice communities, at least over shallow water, are dominated by benthic forms, including benthic diatoms and larvae of benthic organisms (Carey 1985; Horner et al. 1992). Furthermore it is possible to differentiate between ice biocoenoses related to compact pack ice, "ice-edges", and "xenocryobionthic" biota distributed irregularly in the vicinity of the original sea ice biota (Horner 1985b; Melnikov 1997). An extensive food web is supported during the growing season by algae mainly on the undersurface of the sea ice. Dunbar (1977b) described the ice community as a system of high local production embedded within a low-productivity system.

The drift ice zone extends further south in the west of the OSPAR area compared to the east (Fig. 36) due to the currents and related water temperatures (Figs. 15, 34, 35). These patterns are reflected by distribution patterns of smaller ice related biota as well as by large predators such as *Ursus maritimus* (polar bear) and pinnipeds as *Odobenus rosmarus* (walrus), *Erignathus barbatus* (bearded seal), *Phoca groenlandica* (harp seal), *Cystophora cristata* (hooded seal), and *Phoca hispida* (ringed seal) that use drift ice plates as a platform for transport, pupping and resting (*e.g.* Ridgeway and Harrison 1981, 1989a; Hansen et al. 1996).

High concentrations of micro-algae are abundant especially at retreating ice-edges, ice-water interfaces, in ice micro-channels, and at interstitial spaces of the ice bottom of first-year ice and play an important role in the trophodynamics of polar marine ecosystems. Changes in light levels have been shown to be of critical importance for the growths of under-ice algae and would also be a major controlling factor in the diversity of phytoplankton (Hellum 1994). Diatoms, starting in the early spring (– the time depends on light intensity and melting processes and therefore on latitude and seasonality of the location –), further ice algae (*e.g.* Horner 1985b), and following fauna (*e.g.* Carey 1985) browsing on this concentrated food source build the base of the Arctic food web (Melnikov 1997). Summer and autumn plankton have a larger component of dinoflagellates and flagellates and in winter with small flagellates compared to the diatom dominated spring bloom (Hellum 1994). While there are >200 species of sea ice associated diatoms in the Arctic, only two dinoflagellates can be considered to be cryophilic (Okolodkov and Dodge 1996).

As new bottom-ice forms in autumn microalgae are incorporated into the ice and are present in brine pockets and channels throughout the winter. Sea ice microalgae must therefore be able to survive prolonged periods of total darkness at temperatures of -1.8°C or less and have developed different mechanisms to cope with such conditions (Palmisano and Sullivan 1985). With increasing temperatures in spring, brine release from channels occurs and cells are carried towards the bottom of the ice. When light levels at the bottom reach a certain threshold ice algae begin to divide and subsequent form a golden brown layer 3-5 cm thick. Surface and interior ice communities are of minor importance in the Arctic compared to the Antarctic ice biocoenoses. The presence of ice communities early in spring before the phytoplankton start to grow shows that they provide a valuable source of food for planktonic and benthic grazers. While some ice related organisms are only found in sea ice, there are others that also occur in the water column and sediments at high latitudes (Horner 1985b).

In relation to biological processes it is important to differentiate between first-year and multi-year ice. Species abundance, diversity, and productivity in multi-year ice is much lower compared to first-year ice (Fig. 38). Multi-year ice has a much smoother bottom surface than first-year ice (HORNER 1985b; VINJE and KVAMBEKK 1991; LEGENDRE et al. 1992) and also different species of sub-ice amphipods are dominant below those two different types of sea ice (CAREY 1985). Ice algal blooms and spring phytoplankton blooms can be clearly separated in time and sometimes by species present. Species compositions might differ from year to year however and the succession will be influenced by the age of the ice (HELLUM 1994).

Undeformed older ice in the Arctic basin has a thickness of around 3-4 m. Staying in an equilibrium of growing from below and surface melting, the ice does not generally last more than 7 to 10 years. Over an annual circle some 40-50 cm of ice are lost at the surface and replaced by an equal amount of new ice at the bottom (MAYKUT 1985). As snow and ice melt either by increasing air temperatures or higher water temperatures due to currents and drift processes, the ice decays with ice biota and nutrients being flushed into the adjacent waters, giving a high input into the Arctic food web by triggering ice-edge phytoplankton blooms and associated consumption (HORNER 1985b).

But besides this input ice-edge phytoplankton blooms are also supplemented by nutrient cycles between the sediment and the water column with the effect that primary production of the water column above the Arctic shelves is about triple that of pelagic regions and which is evidence for benthic-pelagic coupling processes (Figs. 37, 38) (LEGENDRE et al. 1992; BRANDT 1995; BRANDT et al. 1996). In addition, the influence on benthic communities is different below ice-covered areas compared to pelagic areas without ice due to a different vertical flux of detritus from ice-related communities.
Wind and density driven upwelling might add considerably to an enrichment of nutrients at ice-edges and within polynyas (DUNBAR 1985; LONGHURST 1998). Not only productivity patterns but also species composition gives evidence for a benthic-pelagic interaction in shallow ice cover-influenced regions (CAREY 1985).

Fauna in this upside-down (thigmotropic) benthic environment of the sea ice bottom appears to survive well in the absence of ice in summer but colonises the lower layers of ice as soon as it develops. The food chains extend beyond the ice itself to include zooplankton and fish in the water layer beneath the ice and beyond the ice-edge, also supporting seabirds and larger predators. The true under-ice macrofauna is almost entirely composed of gammarid amphipods, occupying a variety of subhabitats, while calanoid copepods are mainly related to ice-edges.
Inside interstitial spaces and brine channels, the larvae of benthic polychaetes, pelecypods, gastropods, tunicates, turbellarians, cirripeds, nematodes, harpacticoid and cyclopoid copepods, calanoid copepods, and rotifers are meiofaunal members of the Arctic ice-bottoms and ice communities, while ciliate protozoans dominate the microfauna (CAREY 1985). Characteristically the larger herbivorous copepods perform deep seasonal migrations, passing the winter in water as deep as 1000 m, partly associated with the need for several seasons to complete their ontogenetic growths and reproduction cycle (LONGHURST 1998). The amphipods *Gammarus wilkitzkii, Apherusa glacialis*, and *Onisimus sp.* are regarded as autochthonous sea-ice associated fauna (GULLIKSEN 1984; LØNNE and GULLIKSEN 1991a, b).

Protected lagoon/ Embayment fast ice	Shallow water oceanic fast ice	Deep water fast ice	Pack ice
First-year ice sheet	First-year ice	First-year ice	First-year ice
Multiyear ice sheet	Multiyear ice	Multiyear ice	Multiyear ice
Coastal tide cracks	Tidal cracks		
Rough ice	Pressure ridge keels and rough ice	Pressure ridge keels and rough ice	Pressure ridge keels and rough ice
			Edge ice

Fig. 39: Major sympagic faunal habitats in the Arctic and Subarctic (after CAREY 1985).

Arctic sea ice, being a heterogeneous and often patchy environment, forms different habitats (Fig. 39) with different associated faunas which have been characterised by CAREY (1985). Composition and ecology of those animals relies on regional variations of the ice habitat structure. Above that water depth determines not only productivity patterns but also the extent of the fast, unmoving sea ice sheet attached to the shoreline and therefore whether vagile benthic animals can actively migrate between the benthic and under-ice surfaces. At under-ice surfaces above deep water there are different communities of gammarid amphipods, more related to a pelagic origin, than above the shelves, where there is a close relation to the benthos. Thus in addition to the ice structure itself the depth of water is a major criterion and has proven to be a controlling factor in the species composition and structure of ice communities and therefore to differentiate Arctic marine environments (CAREY 1985).

3.5.1 The Northeast Water Polynya

Patches of wider and recurring open water exposures in the pack ice are termed *polynyas* unlike large scale linear, but narrow open cracks that are called *leads* (MAYKUT 1985; SMITH et al. 1990). Polynyas depict oasis-like situations of non-linear open water, young ice, and newly formed ice patches within permanently ice covered environments and thus are of high biological significance (*e.g.* SALOMONSEN 1972; BROWN AND NETTLESHIP 1981; DUNBAR 1981; HJORT ET AL. 1983; HJORT ET AL. 1988; MASSOM 1988; BLEAKLEY and ALEXANDER 1990; FRANCE AND SHARP 1992; HIRCHE AND KATTNER 1994; BRANDT 1993, 1995; FALK AND MØLLER 1995; BRANDT ET AL. 1996; AMBROSE and RENAUD 1995, 1997; PIEPENBURG ET AL. 1997).

While there are two common types of polynyas – the sensible heat or open ocean polynya and the latent heat or coastal polynya (DUNBAR 1981; MASSOM 1988; BEARMAN 1989; SMITH et al. 1990) – the most important polynya for the OSPAR area develops due to a different mechanism of its own (BOURKE et al. 1987; DARBY et al. 1995; GUDMANDSEN et al. 1993, 1994, 1995; MARKUS and BURNS 1995; SCHNEIDER and BUDÉUS 1994, 1995, 1997) (Fig. 41). The kernel of the "Northeast Water Polynya" (NEWP), lies between ~79°-81°30' N on the north-east Greenland Shelf with an opening of 40,000-44,000 km^2 in summer (BRANDT et al. 1996). Opening begins in late spring (May to June) and reaches its maximum extent in late summer. An interaction

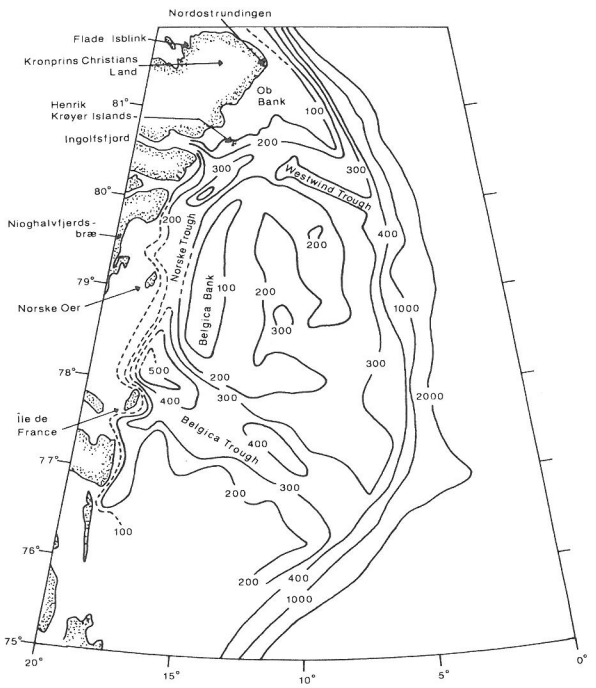


Fig. 40: Topography and bathymetry of the north-east Greenland shelf. Depth contours are in metres - dashed lines in areas covered by fast ice (from SCHNEIDER and BUDÉUS 1997).

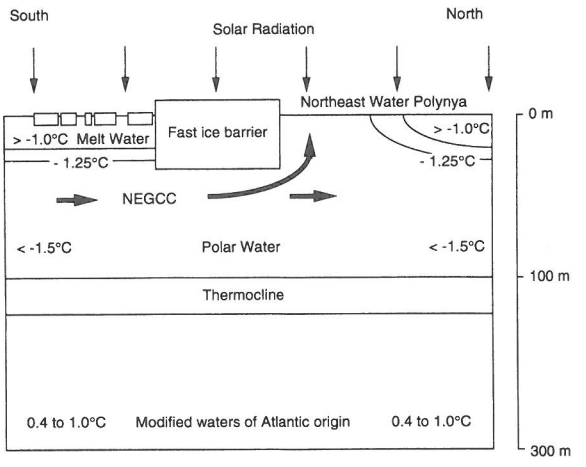


Fig. 41: Scheme of the NEWP formation process (from SCHNEIDER and BUDÉUS 1995).

Opening begins in late spring (May to June) and reaches its maximum extent in late summer. An interaction between the northward bound "North-East Greenland Coastal Current-NEGCC" (Fig. 15) *i.a.* with the fast ice barrier on the Norske Ør Shelf and Belgica Bank (Fig. 40), westerly winds, and the position of the Ob Bank protecting the area from Arctic sea ice import results in open-water formation (Fig. 41) especially in summer when the air-sea heat budged is positive. Wind influence can modify the process considerably towards the north and north of Ob Bank where open water occasionally is formed in summer but presumably also in winter as a latent heat polynya (SCHNEIDER and BUDÉUS 1995, 1997).

Archaeological excavations (ANDREASEN and LANGE 1994; ANDREASEN 1997) assessed prehistoric resource-exploitation at sites close to the polynya coastline. This refers to a human population that must have lived on animal food sources along the north-east Greenland coast in former times and therefore suggests the existence of open water throughout the year. These findings might confirm the assumptions of SCHNEIDER and BUDÉUS (1997) of a presumed existence of permanent open-water spots from the presence of large schools of walruses and seabirds in the area.

The biological importance of recurring polynyas in the high Arctic environment is evident. Polynya open-water patches show markedly differences in primary production compared to surrounding ice covered areas (Fig. 42) (LARA et al. 1994; SMITH 1995; AMBROSE and RENAUD 1997; PIEPENBURG et al. 1997; SCHNEIDER and BUDÉUS 1997). From this production periodicy results a seasonally pulsed POM flux to the seafloor below the open water patches of the polynya, but which is not necessarily related to reproduction cycles (LARA et al. 1994; BAUERFEIND et al. 1995; SMITH et al. 1995; AMBROSE and RENAUD 1997).

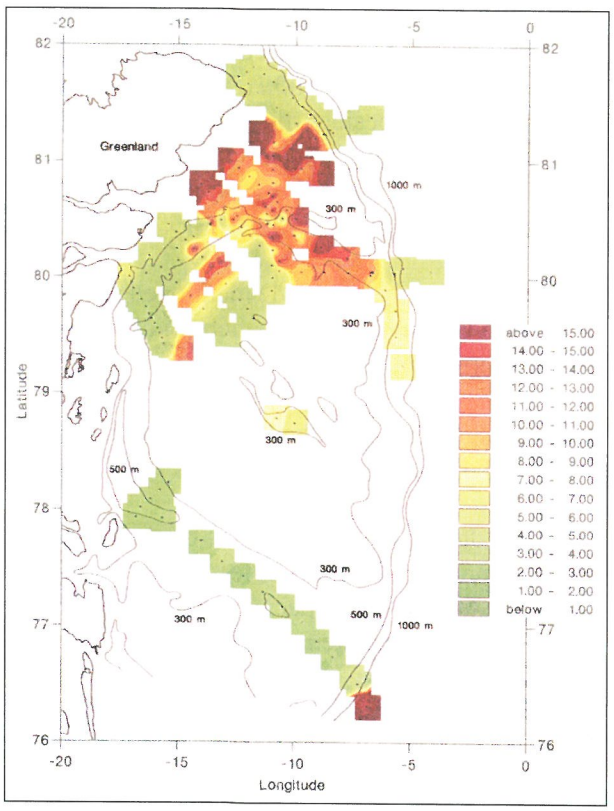


Fig. 42: Integrated (upper 50 m) Chlorophyll fluorescence in relative units (from SCHNEIDER and BUDÉUS 1997).

AMBROSE and RENAUD (1995) as well as ROWE (1996) used the NEWP as a model to predict potential productivity of pelagic and benthic communities, seasonal pulses and sizes of different foodweb components (DEMING et al. 1995; NEWTON and ROWE 1995), and hence pelagic-benthic coupling in polar regions and found markedly higher biomass, benthic infauna (meiofauna), macrofauna (polychaete) abundance, and sediment carbon concentration under ice-free areas of the NEWP. The mechanism of seasonal pelagic-benthic coupling and its high significance for production, abundance and diversity was also highlighted by PIEPENBURG et al. (1997).

The relationship between species composition of the peracarid fauna (Crustacea, Malacostraca) and hydrographical processes influencing the NEWP production (benthic-pelagic coupling) have been described and confirmed by BRANDT (1995) and BRANDT et al. (1996). These authors identified seven species assemblages not primarily reflecting bathymetry but nutrient supply related to oceanographic factors within the polynya area and the temporal and spatial opening of the polynya triggering primary production and benthic-pelagic coupling processes. BRANDT (1995) concluded that environmental conditions must have been stable over a long period of time to develop the high peracarid biodiversity identified by her.
A comprehensive report of a 1993 cruise (ARK IX/2 and 3 expeditions) to the NEWP, comprising preliminary reports of research *i.a.* on micro-, phyto-, zooplankton, benthos, marine mammals, birds, and archaeology, is given by HIRCHE and KATTNER (1994). These reports underline the high biological evidence of the NEWP.

While the North Water and other recurring polynyas of the Canadian Arctic archipelago are widely known for their importance in providing winter refuge for marine mammals as well as for their properties as staging grounds for feeding and reproduction of migrant birds during spring (DUNBAR 1981; MASSOM 1988; FRANCE and SHARP 1992), the NEWP has gained much less attention to its significance for marine mammals in the past. This might have been due to its more remote and isolated situation off north-east Greenland within a massive permanent pack ice belt (Fig. 36). Different subprojects of the ARK IX/2 and 3 expeditions (HIRCHE and KATTNER 1994) reported the abundance of *Ursus maritimus*, *Phoca hispida*, *Erignathus barbatus*, *Monodon monoceros* (narwhale), and *Odobenus rosmarus* in the NEWP area with latter being the most numerous sea mammal. *Cystophora cristata*, and *Phoca groenlandica* were counted only in low numbers from helicopter survey.
The highest significance for higher taxa related to the NEWP is given for Arctic seabirds. Larger colonies of *Rissa tridactyla* (black-legged kittiwake), *Fulmarus glacialis* (northern fulmar), and a smaller colony of *Larus hyperboreus* (glaucous gulls) are located in the vicinity of the NEWP. The fulmars are exclusively of dark colour-phases (HÅKANSSON et al. 1981; FRANEKER and WATTEL 1982; FALK and MØLLER 1995). In addition Hjort et al. (1983) made records of *Somateria mollissima* (common eider duck), *Somateria spectabilis* (king eider), *Pagophila eburnea* (ivory gull), *Sterna paradisea* (arctic tern), *Gavia stellata* (red-throated diver), *Charadrius hiaticulata* (ringed plover), *Calidris canutus* (knot), *Calidris alba* (sanderling), *Stercorarius skua* (great skua), *Xema sabini* (Sabine's gull), *Rhodostethia rosea* (Ross's gull), and *Stercorarius longicaudus* (long-tailed skua) besides migrating *Arenaria interpres* (turnstone) and non-marine birds. Bird records were largely supplemented in later surveys (HJORT et al. 1987, 1988; HIRCHE and KATTNER 1994). South of the NEWP kernel a new colony of northern fulmars has been reported near a small coastal polynya at Mallemukfjeld (FALK and MØLLER 1995).

BROWN and NETTLESHIP (1981) mentioned another smaller recurring polynya at Scoresby Sound in the middle of the east Greenland coast, where thick-billed murres/*Uria lomvia* breed besides black-legged kittiwakes and northern fulmars.

SMITH et al. (1990) described the formation process of the "Whaler's Bay Polynya" which is a sensible heat winter polynya above the shelf break north of Svalbard.

Darkness during the polar winter might hinder birds in foraging or perhaps as research might reveal the ability of northern seabirds to feed in the dark. Since small numbers regularly winter at high latitudes in the Canadian Arctic, some species are evidently able to forage efficiently enough to at least meet their energy requirements for maintenance (BROWN and NETTLESHIP 1981).

Open water leads measuring several kilometres have been frequently reported from the central Arctic in summer. A decreasing trend in sea ice volume has been detected from shipboard, satellite, and submarine measurements at least for the last forty years (AWI 2000). This was particularly the case in the summers of 1996 and 2000 which had a comparatively poor Arctic polar sea ice cover with reports of open water patches at the North Pole itself.

4 Biogeography

4.1 Definition

The definitions given below give an outline of the range of ideas and tasks (marine) biogeography has to deal with.

"Every species has three maxima of development, in depth, in geographic space, in time.
In depth we find a species first represented by a few individuals, which become more and more numerous until they reach a certain point, after which they again diminish and at length altogether disappear. Provinces, to be understood, must be traced back, like species, to their history and origin in past time" (FORBES 1859).

"Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare, and, as I believe, the future success and modification of every inhabitant of this world" (DARWIN 1859).

"Biogeography is the study of biological patterns that can be mapped" (MACARTHUR 1972).

"A phytogeographical region is a stretch of coast with a relatively homogenous flora, which is separated from other such parts with different homogenous floras by floristic discontinuities, which may coincide with comparatively small stretches of coast with a rapidly changing flora or with marine or terrestrial barriers" (VAN DEN HOEK 1975).

"Biogeography can be defined as the study of dispersal and patterns of behaviour of organisms in space and time" (COX et al. 1973) or as stated later "Biogeography is the study of living things in a spatial and temporal context" (COX and MOORE 1995).

According to Earll and Farnham (1983) biogeography has three recognised goals:
1. The delineation and characterisation of each distinct faunal or phytal area
2. The attempt to trace the history of the faunas
3. The use of zoo(phyto)geographic data to augment our knowledge about the course of evolution.

"Biogeography is the study of the distributions of organisms, both past and present, and of related patterns of variation over the earth in the numbers and kinds of things" (BROWN and LOMOLINO 1998).

BRIGGS (1995), in his review of past biogeographic approaches, gave an outline of the historical development of (marine) biogeography from its beginnings, with special emphasis on the relation to vicarianism, geology, and plate tectonics.

Marine biogeography of the OSPAR area has to reflect patterns regarding evolution and ecological conditions during certain geological time scales, from the littoral down to abyssal depths of more than 5,500 m, and from the permanently ice-covered Arctic Ocean over seasonal shifting ice edges, vast pelagic spaces with different currents and water masses in different depths, and along shelves under different temperature regimes and with different substrates.

4.2 Biogeography in marine environments

The oceans contain ~97% of the world's water ($\cong 1455*10^6$ km^3), they cover ~71% of the world surface, and 88% of the oceans are deeper than 1000 m, resulting in an average depth of 3800 m of the world ocean. About two-thirds of the biosphere are occupied by bathyal and abyssal depths (BRIGGS 1995).

In contrast to terrestrial biogeography, the physical properties of water create a very different situation over a much wider vertical range in the fluid and three-dimensional marine environment making research and description of marine patterns more difficult. Vertical delimitation of species distribution is even more difficult over such a wide latitudinal range due to the phenomenon of polar emergence and tropical submergence in thermal étages (LE DANOIS 1948; ZENKEVITCH 1948/1949; EKMAN 1953; HEDGPETH 1957; DE LATTIN 1967; MENZIES et al. 1973; VAN DER SPOEL and HEYMAN 1983; GLÉMAREC 1973, 1988; LONGHURST 1998).
In addition the basis of the euphotic epipelagial and the topographical shelf break at ~200 m depth is not a clear vertical boundary for many shallow water, mesopelagic, and eurybathymetric pelagic and benthic species (MENZIES et al. 1973; CARNEY et al. 1983; ZEZINA 1997) (Chap. 6.1).

On a global scale, terrestrial biogeography is principally a geography of vegetation arrangements, whereas marine biogeography is dominated by faunal distribution patterns. Biogeographical and ecological systematics related to terrestrial biomes (*e.g.* UDVARDY 1975, SCHULTZ 1995) are commonly based on certain patterns of plant growth and distribution. Latitudinal differences in the radiation budget, the availability of water and other climatic quantities which – together with the local geology – create certain soils upon which specific patterns of vegetation communities and structures develop. Such sociological patterns of phyto- and dependant zoocoenoses are present on the more or less two-dimensioned terrestrial surface in a comparably narrow vertical zone of an atmospheric environment.

Marine environments are totally different due to the different physical properties of the water, *e.g.* different depths of light penetration and absorbency of the radiation spectrum with vertical and latitudinal gradients; gradients in density; differences in salinity; different conductivity and capacity of energy; differences in oxygen contents and in the distribution of nutrients respectively; different currents in different water masses in different depths; ice cover and ice-water interfaces; ... . The distribution of many of these factors is, however fairly predictable these days.
These factors create a three-dimensioned situation over a much wider vertical range in a fluid environment and terrestrial biogeographic boundaries cannot be transferred directly to the marine environment (Fig. 43) (DUNBAR 1979; PIELOU 1979; HAYDEN et al. 1984), even though terrestrial and marine spheres are merging in very shallow and semi-aquatic coastal biotopes (PIELOU 1979; VALENTIN and JABLONSKI 1983; PRICE and HUMPHREY 1993). Another consideration is that the fluid medium provides a continuous character and boundaries are rarely sharp.

In contrast to terrestrial biogeography where plants are used as naturally fixed indicators for specific ecological and environmental factors, seaweeds and seagrasses as marine macrophytic counterparts, might be only of use in sublittoral depths.
The majority of marine primary producers are pelagic phytoplankton and therefore might be moved from optimum conditions/locations by currents. Microalgae and zooplankton are able to survive being carried hundreds of kilometres and can be found in substantial quantities far beyond their ecological reproduction limits (*e.g.* VAN DER SPOEL and HEYMAN 1983; ANGEL 1993;). Even planktonic larvae of adult benthic sessile fauna drift over wide areas.

Marine biogeographic delimitations might differ considerably or can be quite contradictory – as shown by some examples below (Chaps. 5.1 ff.) – not only according to different ideas or methods of biogeographers but also between flora and fauna, benthos and pelagos, or different taxonomic groups. For instance a very large fraction of the class Polychaeta is considered to be eurybath and or eurygraph (see Chap. 4.3) and their geographical distribution usually deviates from that of other marine taxonomic groups (FAUVEL 1959; HOLTHE 1978).

One similarity to terrestrial biogeography is that there are latitudinal belts of biogeographic zones on the global scale (*e.g.* Figs. 43, 48, 55, 60, 62-64). These are principally influenced by patterns of solar radiation (Chap. 3.4) and currents (Chap. 3.3) that distribute characteristics of marine climates into the pelagial and shallow benthal of latitudes under other atmospheric climate regimes (*e.g.* VAN DER SPOEL and HEYMAN 1983; COUPER 1989; BAILEY 1996).

There is a general latitudinal gradient of a decrease in pelagic, benthic, and even in deep-sea species diversity from the equator to the poles *e.g.* for isopods, brachyura, bivalves, and gastropods (CHRISTIANSEN 1982; ANGEL 1993; REX et al. 1993; VERMEIJ 1996). On the other hand no diversity decline – only different diversity patterns – could be found in northern North Atlantic and Arctic waters for amphipods by BRANDT (1995), BRANDT et al. (1996), and WEISSHAPPEL and SVAVARSSON (1998).

Biogeographic patterns are very broad in the oceanic pelagial and deep-sea (Figs. 104, 107) due to the more uniform environmental conditions, whereas they are more linear and belt-like along continental slopes and shelves due to the geophysical structure. This gets more patchy inshore due to more various influences in shallow near coast environments with possible disjunctions by a variety of factors such as geological features, tidal interactions, and riverine outflows (ANGEL 1993).

In deep-sea environments, under aphotic conditions (Fig. 12), plants are absent and only faunal and micro-organisms are of use for biogeographical classifications in the vertical dimension.

These issues illustrate the widely different features in biogeochemical cycles and spatial distribution patterns of marine species that have to be taken into account. They affect the determination of boundaries and therefore make them difficult to define.

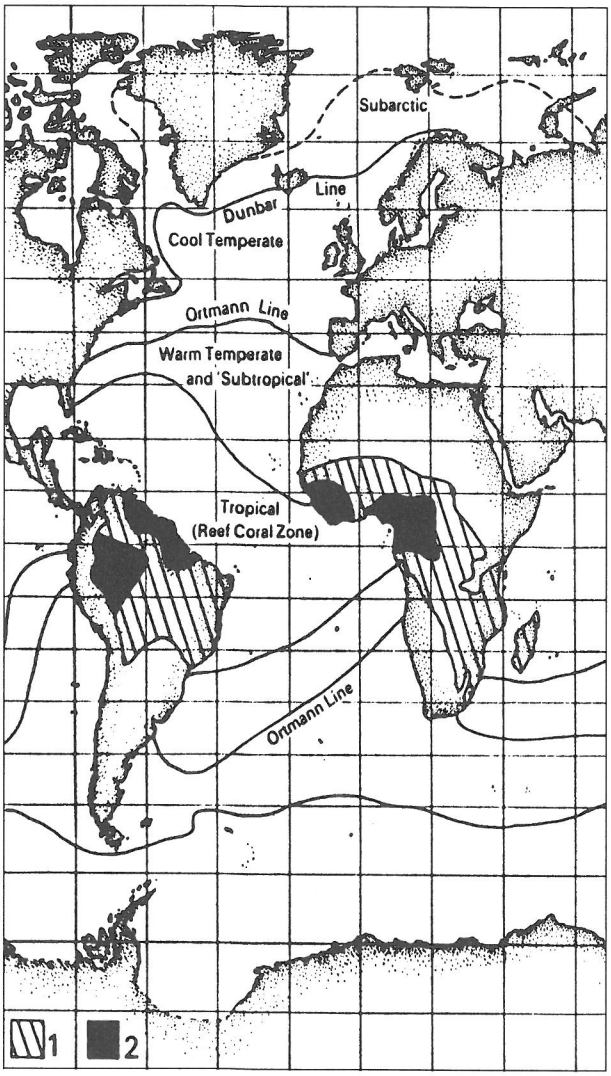


Fig. 43: The marine biogeographic zones with tropical rainforest (black) and savannah (hatched) on the continents (from Dunbar 1979).
Dunbar line = average 5°C surface isotherm
Ortmann line = average 15°C surface isotherm
Tropical zone = in-between 25°C surface isotherms

The presence of a biological community might reflect a set of known or unknown environmental conditions that constitute the ecological niche of its members in the examined area. Besides a sound taxonomic discrimination, non-taxonomic attributes, such as numerical abundance, biomass, size spectra feeding types metabolic rates, biotic (trophic relations, competition, predation, succession) interactions could also be used to describe the structure and function of communities (SCOR 1994).

Marine biogeography has been subject of scientific studies for more than one and a half centuries but looking at the very different approaches and uncertainties, it might be stated that it is still far from being sufficiently explored. Even though records of marine organisms have improved considerably within the last decades, knowledge about distributional patterns of taxa and in the vast oceanic spaces still remains very poor compared to terrestrial organisms.

Some judgement and courage is needed to fix dynamic biological features operating on such a scale as (pseudo) static facts on a map.

4.3 Biological types of marine distribution

The distribution of marine organisms depends on ecological barriers as stressed by BĂNĂRESCU and BOŞCAIU (1978), as well as on palaeogeographic and evolutionary circumstances as indicated in chapter 3.1. The ecological barriers are different for littoral, pelagic, benthic intermediate deep, or abyssal species. For example oceanic areas and abyssal depths might act as ecological dispersal barriers for littoral organisms whereas shallows in non-polar latitudes hinder the distribution of abyssal species (*e.g.* DE LATTIN 1967; BĂNĂRESCU and BOŞCAIU 1978).

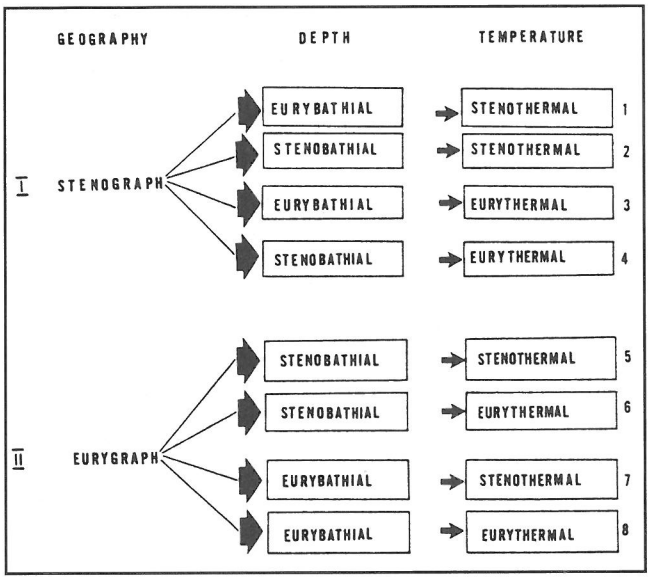


Fig. 44: The eight basic types of marine species distribution (from MENZIES et al. 1973).

The matrix of marine distribution types of MENZIES et al. (1973) (Fig. 44) illustrates eight possible combinations based on the autecology of species with regard to their distribution in the three-dimensioned marine environment.
Stenobathial was defined as indicating species with a vertical range of < 300 m or 10% average ocean depth whereas stenothermal describes species confined to one marine climate (*e.g.* boreal or tropical). The range in salinity is so narrow throughout the oceans – with the exception of estuarine situations or some Low Arctic locations – that most marine species were considered as being stenohaline and salinity thus not judged as a distribution limiting factor. Thus marine organisms can either be eurypotent or stenopotent related to environmental factors as depth/bathymetry and temperature with a combination of those basic types to a different extent leading to two general types of geographical distribution.
For example VERMEIJ (1991) accentuated that the 295 trans-Arctic molluscan species having invaded from the Pacific during the Pliocene do show a significantly broader geographical range than do taxa with a pre-Pliocene history in the Atlantic. Additional factors and causes for geographical restriction possibly leading to speciation or extinction which have been suggested include anoxia (of deeper waters), trophic restriction, competition and predation, regression and habitat loss, and climate change (cooling) (VERMEIJ 1989).

Most deep-sea but also many pelagic organisms are eurygraphs with a wide geographical distribution due to the rather uniform conditions in these environments (type 7). On the other hand do such endemic organisms with stenothermal and stenobathyal potencies, and therefore often with a restricted geographical distribution (stenographs), have a high indicative value for environmental conditions and related biogeographic delimitations. According to MENZIES et al. (1973) and concerning figure 44 many animals of various phyla in the nearly isothermal (hypopsychral) High Arctic are typical for type 1 (stenographs, eurybaths, stenotherms). Type 2 (stenographic, stenobathial, stenothermal) fauna can be either of a stenobathic-shallow-water or stenobathic-deep-sea subtype (*e.g.* the isopod *Macrostylis affinis* in the deep N-Atlantic). Eurybathial, eurythermal stenographs (type 3) are uncommon and only seen in a few locations where shallow water organisms extend into moderate deep (archibenthal) zones (*e.g. Desmosoma laterale* in the Skagerrak). Type 4 (stenographic, stenobathial, eurythermal) animals are exclusively seen in middle or lower latitude shallow marine environments, where significant changes occur in the ambient temperature. Stenobathial, eurythermal eurygraphs (type 6) are depicted by a large number of intertidal, shelf, and epipelagic planktonic forms with bipolar or cosmopolitan distribution. Most deep-sea animals belong to type 7 (eurybaths, stenotherms, eurygraphs) with a wide geographic and bathymetric distribution within the cold stenothermal environment of the deep-sea. Some low polar species have successfully invaded adjacent High Arctic, boreal or temperate regions on a wide bathymetric amplitude and are therefore regarded as type 8 (eurybaths, eurytherms, eurygraphs).

4.4 Temporal and spatial scales

Biogeographic patterns have never been static and stable when looked at over geological time scales as described in the chapters 3.1 and 3.4 regarding plate tectonics, climate change, adaptation, speciation, vicariance, and evolution or on a lower level due to changes in upwelling regions, currents, or due to salinity anomalies as discussed in chapter 7.

Hierarchy of factors	Geographical scale Global	National	Regional	Local
Spatial				
1. Climate–latitude (e.g. precipitation, seasonal variations in day length, ice cover)	+++	+++	++	+
2. Sea temperature (e.g. surface isotherms)	+++	+++	++	*4b
3. Global residual water movements – ocean currents	+++	+++	++	+*6
4. Water quality				
(a) Nutrients	++	+++	++	++
(b) Temperature regime, seasonal/depth	+	+++	++	++
(c) Salinity	+	+++	++	++
(d) Turbidity	–	+++	++	++
(e) Other chemical factors	–	+	+	+
(f) Biological qualities (difficult to measure)	–	+	+	+
5. Coastal geology				
(a) Topography	+	+++	+++	+++
(b) Substratum	++	+++	+++	+++
6. Water movement				
(a) Wave action	–	+	++	+++
(b) Tidal currents	–	+	++	+++
7. Local effects When they occur +++, e.g. thermal effluent, harbour effects, freshwater input				
Temporal				
1. Short-term (to 100 years), e.g. Russell cycle – boundary dynamics, coastal ice patterns		+++	++	+
2. Long-term (to 10 000 years), e.g. glaciation effects	+++	+++	++	+
3. Events – non-cyclical phenomena, e.g. wrecks, artificial environments (Mt St. Helens, Surtsey), alien species when they occur +++				

Global: extent 5000+ km (*e.g.* NEA);
National: extent 1000+ km (*e.g.* British Isles);
Regional: extent 200+ km (*e.g.* the west of Scotland);
Local: extent 20+ km (*e.g.* Anglesey);

weighting of environmental factors:
+++ A primary factor, recorded and studied in detail;
++ A significant environmental factor often recorded and described in detail;
+ A secondary factor, seldom recorded and occasionally described;
— Not usually recorded or described;

Fig. 45: The importance of environmental factors (spatial and temporal) in relation to geographical scale. Spatial factors are ranked in importance in determining species geographical distributions (from EARLL and FARNHAM 1983).

Global effects of man-made changes concerning the marine environment such as climate change or intensive large scale industrial fisheries might even increase the rate of change in patterns of marine biodiversity. Although having discussed ancient biogeographic patterns (*e.g.* Chap. 3.1, Fig. 7) the classification resulting from this study should reflect the present biogeographic situation.

Biogeographic patterns can differ depending on the spatial scale at which it is considered (*e.g.* Figs. 45, 46). The scales dealt with in this study are indicated in chapter 4.4 and are clarified further by the maps (compare the Figs. 104, 105, 106, 107) of the biogeographic classification.

EARLL and FARNHAM (1983) presented a scheme which correlated spatial and temporal environmental factors with possible scales of biogeography (Fig. 45). To these authors all scales they described and which should be statistically proportioned are "biogeographic". It was highlighted that the isolation of the influence of a particular environmental factor on biogeographic patterns in practice proved to be difficult. The larger-scale factors mentioned in figure 45 have been discussed above in this study.
HAURY et al. (1977) as well as VAN DER SPOEL and HEYMAN (1983) regarded coarse and meso-scale patterns as being the most important ones for pelagic zoogeographic studies despite macro- and mega-scale patterns being substantially pelagic zoogeographic patterns (Fig. 46). According to these authors, hydrographic, ecological, behavioural factors, and zoogeographical (planktological) patterns are most distinctive influenced at the former scales. Regarding coarse- and meso-scale zoogeographic patterns of plankton there has generally been so far a focus on the distribution of single species (VAN DER SPOEL and HEYMAN 1983).

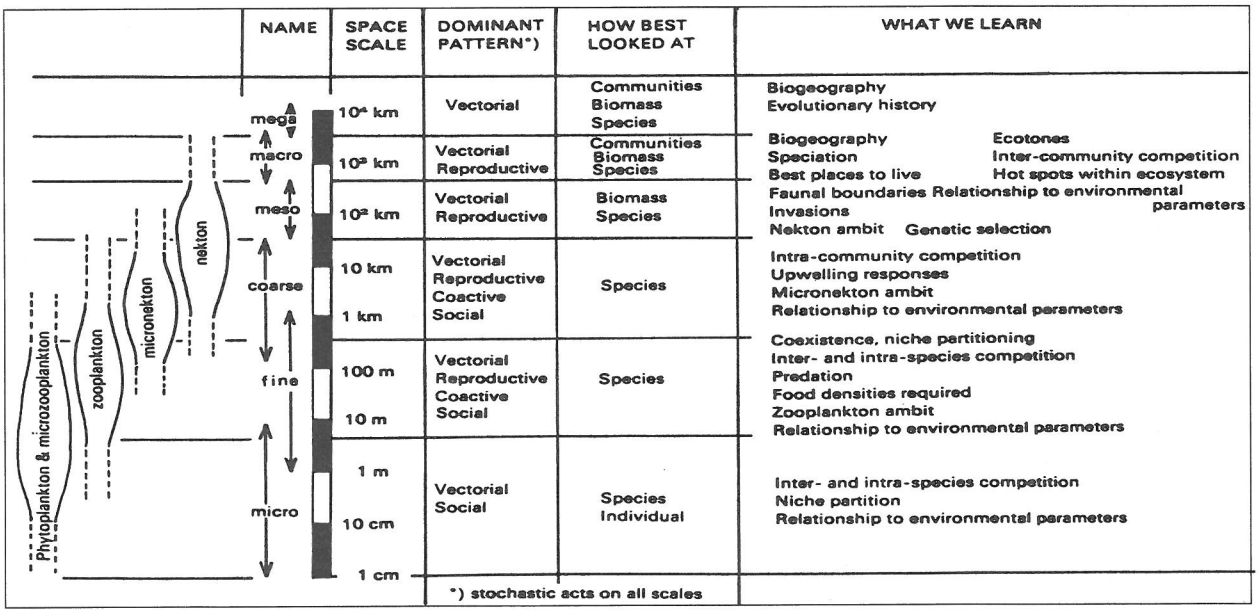


Fig. 46: Spatial scales of pelagic biological patterns (from Haury et al. 1977; VAN DER Spoel and Heyman 1983).

5 Examples of different approaches to marine biogeography of the North-East Atlantic

"The biogeographic method does not exist, or there are as many methods as biogeographers"

This heretical statement was made by DUNBAR (1979) and LONGHURST (1998) and seems to be true at least for marine environments.
EARLL and FARNHAM (1983) added that it was not unusual for biogeographic workers considering different environmental groups, for example benthic or planktonic organisms, or particular taxa to produce rather different boundaries for biogeographic provinces or, as HEDGPETH (1957) stated, that each worker has his own criteria.
More recently GOLIKOV et al. (1990) argued that the approaches of different researchers to understanding regularities in the distribution of organisms can be quite contradictory, depending not only on differences in the problems facing them, but also on the incompatible methodologies used by biogeographers.

Technical progress has brought major advances in marine biological research and supplies enormous amounts of data but there are still huge gaps in knowledge about distribution patterns of marine organisms especially of the oceanic pelagial, the deep-sea, and of high polar regions. Despite this, BRIGGS (1995) noted that such a vast amount of literature about the distribution of various marine species had appeared in the previous twenty years (until 1994), that he was no longer able to do justice to it in a single book or to discuss the evidence for every biogeographic subdivision. Concerning older biogeographical classifications EARLL and FARNHAM (1983) stated that only few regional faunas could be applied with much success to the shallow sublittoral zone for various reasons before the mid-1970s:

- Virtually all were compiled before SCUBA became widely used and so a number of taxa, especially those living on (nearshore) rocky habitats, had been under-recorded, *e.g.* sponges and ascidians.
- Most did not embody the major taxonomic survey and revisions in the 1970s.
- Extensive areas of coastline between major marine stations had often been undescribed.

Progress in marine taxonomic and spatial research will of course also have its effects on views concerning endemics, *e.g.* whether a taxon considered to be endemic is really endemic to a certain area or whether distribution patterns have previously not been sufficiently explored.
At this point, also the question of modern species definitions has to be taken into account. Species that are acknowledged in their taxonomic status by morphological attributes today and that seem to have a certain distribution might have smaller and different distribution ranges if they turn out to be composed of several genetically different species.

Thus modern marine biogeographic classifications have to reflect problems arising from past descriptions and the technical limitations of the past. According to BRATTEGARD (pers. com.) and other authors the problems of the ever changing (mostly increasing) number of accepted species and the steadily increasing number of invalid names (synonyms) in this context have to be stressed:

- Cases of one species with a distribution range over a large area that turns out to be composed of several species (*e.g.* in the groups of hydroids, polychaetes, molluscs, bryozoans, echinoderms)
- Cases of many different species having been described over past years and decades that, by using modern techniques, turn out to be only one or a few species (*e.g.* the Arctic holothurian *Molpadia borealis* M. Sars, 1859).

Modern biogeography has therefore to reflect these considerations and taxonomic distribution data have to be verified by valid and regularly updated taxonomic registers (compare *e.g.* the European Register of Marine Species/ERMS [EU – Marine Science and Technology Programme/MAST], http://www.erms.biol.soton.ac.uk; North East Atlantic Taxa database/NEAT [Tjärnö Marine Biological Laboratory/Sweden], http://www.tmbl.gu.se/libdb/libdb.html).

The next chapters show that there are many approaches to this discipline. Biogeographic distribution patterns shown by one group of plants or animals or regarding different regional or spatial aspects or by a certain biogeographic technique can be quite different from the patterns shown by another group, region, or vertical zone. Without trying to create a complete listing one can distinguish the following approaches which can be combined in any combination:

taxonomic (selected organisms on different taxonomic levels),
regional,
spatial (*e.g.* only for a certain vertical zone),
evolutionary (phylogenetical) and palaeoecological,
biophysical and oceanographical,
theoretical,
economic (*e.g.* for fishery or seaweed culture),
ecological (considering *e.g.* productivity, or special habitats as hydrothermal vents, seamounts, or ice),
autecological,
purpose guided (*e.g.* for nature conservation),
and vicariance (cladistic) *versus* dispersal approaches.

To arrive at a sound marine biogeography an integrated biogeographical approach should take account of most of the biogeographical disciplines listed above. In particular it should integrate distribution patterns of different biocoenoses and taxa of both flora and fauna, of sessile and mobile organisms with their varied ecological requirements over a given geographical/oceanographical range and a three-dimensioned space, should reveal relationships to geology, geomorphology, and oceanography and should also take into account evolutionary, palaeoecologial, palaeo-oceanographic, and palaeoclimatic aspects. Such an extensive biogeographic classification is still missing, would afford huge efforts, and it is arguable if it ever will be possible to integrate such diverse patterns and all these factors.

5.1 Selected examples of different approaches to marine biogeography:

Most marine biogeographic divisions for the high seas show a rough correlation with the latitudinal marine climatic belts (*e.g.* VAN DER SPOEL and HEYMAN 1983; COUPER 1989; BRIGGS 1974/1995; BAILEY 1996; HÖLZEL 1998; LONGHURST 1998;), even though broad transitional areas have to be presumed (HEDGPETH 1957).

In the following description of different biogeographical classifications some maps (FORBES 1859; BRIGGS 1974/1995–PELAGIAL; BRIGGS 1974/GÖTTING, KILIAN, AND SCHNETTER 1982–COASTAL REALMS/BENTHAL; HAYDEN, RAY, and DOLAN 1984; GBRMPA, IUCN, AND WB 1995; HISCOCK 1998; LONGHURST 1998; VAN DEN HOEK 1975; ZENKEVITCH 1963; VINOGRADOVA 1979) have been transferred into the stereographic projection of the OSPAR area for a better presentation of this particular area. Where possible the design of the original presentation has been maintained but sometimes formerly uncoloured maps have been coloured to help differentiate between different units.

5.1.1 FORBES and GODWIN-AUSTEN (1859): *A natural history of the European Seas*

Building on the early approaches of *e.g.* LOVÉN (1846) and WOODWARD (1856) it was probably Edward Forbes who started marine biogeography as a subject of science in the 19th century with his publication, completed posthumously after his early death by R. Godwin-Austen.
The outcome of Forbes' extensive dredging experience and information brought together from around Europe combined with geological and palaeoecological reflections resulted in a quite detailed descriptions of regional species distribution, aspects of ecology, and seabed characteristics that would be described today as communities and biotopes.
Forbes, being of Scottish origin, named a large province that covered the Irish, British, and southern North Sea coasts and even the entire Baltic Sea as being Celtic and also introduced the term Lusitanean for the warm temperate province in the eastern north Atlantic, Mediterranean, and Black Sea. He further subdivided the seas into 5 zones of depth.

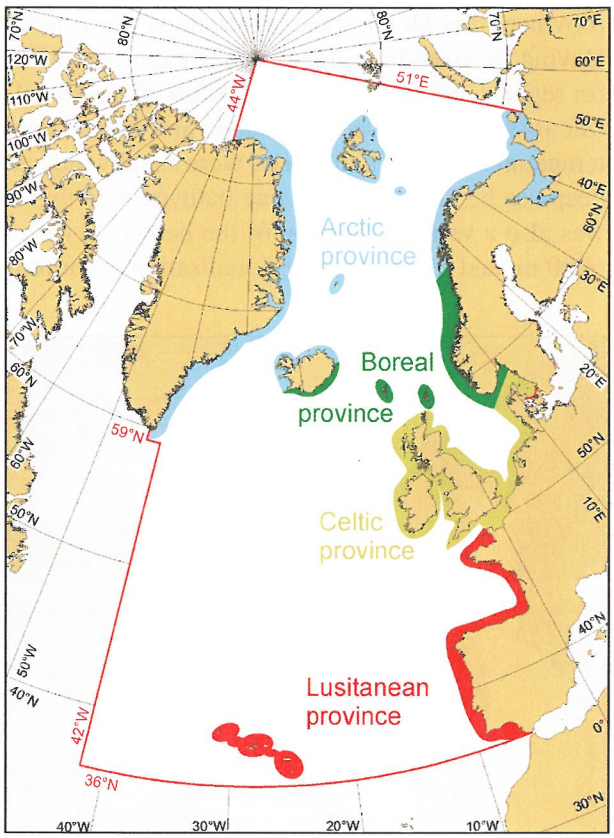


Fig. 47: Biogeographical provinces of FORBES (1859), redrawn in a projection of the OSPAR area.

5.1.2 EKMAN (1935/1953): *Zoogeography of the Sea*

The work of Ekman (in an earlier German and later revised English version) has long been a key text for marine biogeographers.
Combining faunistics with taxonomy, ecology with its fundamental science, physiology, oceanography, present and past climatology, geology, geomorphology, and palaeontology, his comprehensive summary of the distribution of many groups was primarily systematic and regional in scope rather than quantitative.

It may be significant that Ekman, even though he has been cited by most marine biogeographers, did not present any map of a biogeographic regionalisation showing boundaries of the major divisions he described. This was probably due to the fact that biological boundaries in the water are mostly continuous and gradually changing in space and time and therefore ill-defined as a line on a map. For the North-East Atlantic, the palaeoconditions and present species distribution were described for faunas of the Mediterranean-Atlantic warm water shelf, the European Boreal North Atlantic, the Arctic, a Polar-Arctic subregion, the Deep-Sea (Atlantic, Arctic), the Epi- and Bathypelagial.

Ekman stressed the importance of a hierarchical ranking within taxonomic levels and their phylogenetic relationships. He also considered ecological adaptations and the use of statistics to characterise certain geographical delimitations which reflect historical changes in community structures due to changing environments.

5.1.3 BRIGGS: *Marine Zoogeography (1974) / Global Biogeography (1995)*

For many years the classification prepared by BRIGGS (1974) supplemented EKMAN's (1935/1953) work as standard literature for marine biogeography. In other publications (*e.g.* BRIGGS 1966, 1970, 1984, 1987, 1994) he had already stressed the role of geology and related evolution for speciation processes ("vicarianism"), dispersal, and biogeography.
Distinguishing between pelagic and benthic realms, Briggs published a marine biogeographic classification and maps that were only slightly different in 1995. The North-East Atlantic had been divided into three

provinces, the Mediterranean-Atlantic (Warm-temperate), the Boreal (Cold-temperate), and the Arctic. Having focussed his work to a large extent on finfish he referred to endemism rates for invertebrates and fish for regions and provinces and reinforced his faunal boundaries with the rather similar floral delimitations of MICHANEK (1979). Oceano-pelagic and coastal benthic boundaries merge into each other and latitudinal or temperature related boundaries were usually indicated at places of greater change in the inshore biota. For the deep-sea he only proposed one bathypelagic region covering all the oceans except the Arctic basin. There was also a vertical zonation of the benthos with one zone from 200-2000 m, and an other one from 2000-6000 m, and a horizontal regionalisation according to VINOGRADOVA (1979) (Fig. 6.1.2.6).

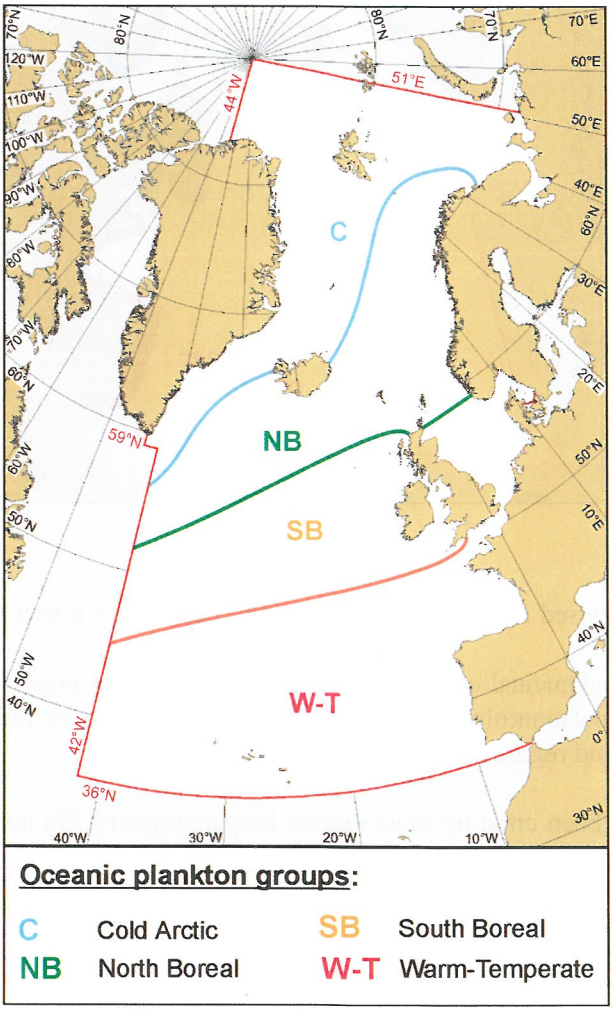


Fig. 48: Pelagic Realm (after BRIGGS 1995, redrawn).

Comment: The 1974 classification from Briggs showed only one zone of Cold-temperate waters which comprised the North and South Boreal zones of 1995. The North Sea seems to be classified Warm-temperate now but was part of the Cold-temperate waters before. This inconsistency might be due to cartographical inexactness concerning the northern warm-temperate boundary. Presumably the North Sea should be then in the South Boreal zone.

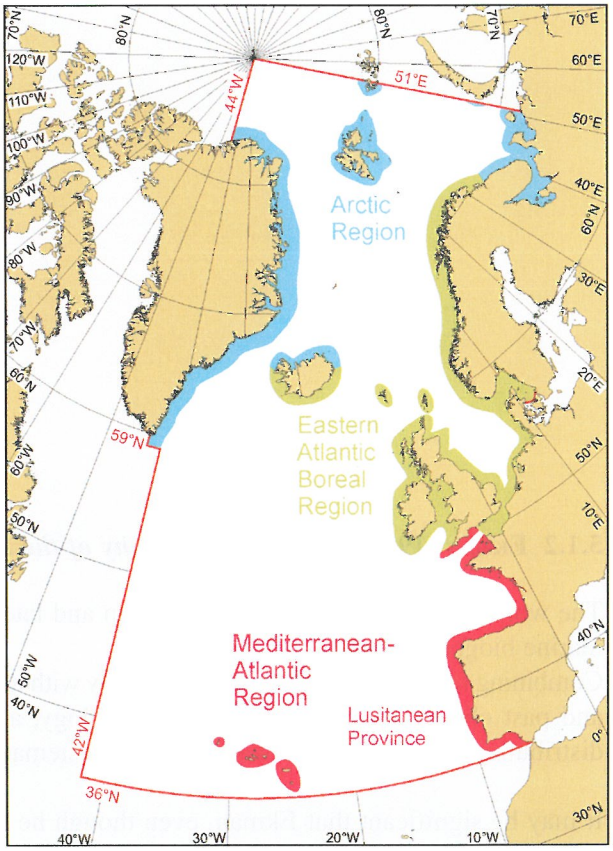


Fig. 49: Benthal/Coastal Realms (after BRIGGS 1995, redrawn).

Comment: The 1974 classification of Briggs for Coastal Realms did not incorporate the English coast along the western English Channel in the Lusitanean province.

5.1.4 DAY and ROFF (1999): *Planning for Representative Marine Protected Areas: A Framework for Canada's Oceans*

In this approach, modified by ROFF and TAYLOR (2000), a stringent hierarchical classification system has been developed. According to the authors, this should make it possible to predict the expected marine biological inventory on the basis of physiographic features related to the specific level of enduring or recurrent habitat characteristics (Fig. 50). Based on ecological principles, the determination of the physical habitat type diversity should basically be related to a community-level analysis of marine systems.
Using GIS software, the different levels of the hierarchy could be overlain with each other to produce seascape-level boundaries.
At the lowest level of the hierarchy (level 8), seascape units are defined.
At level 6 natural regions can be distinguished, here defined as broad oceanographic and biophysical areas characterised by similarities in water-mass characteristics and sea-ice conditions.
At the lower levels of the hierarchy, the seascape-level parameters are applicable to either the pelagic or the benthic ecological realm. These criteria of stratification, slope, exposure and substrate are merged into the GIS with the natural region boundaries. The combination of a pelagic layer overlying a benthic layer forms ecologically unique conditions. Each set of unique conditions defines a habitat type, or seascape, creating the basic functional unit of the hierarchy. Each seascape, therefore, has a unique set of characteristics formulated from the combination of all levels of the hierarchy.

Biological Factors	Oceanographic Factors	Physiographic Factors
Predation	Productivity	Geological activities
Resources (nutrients and food)	Water masses and salinity	Geographical position and latitude
Competition	Temperature	Geological history of the ocean basin
Life-history patterns	Temperature gradients, temperature anomalies and upwellings	Water depth
Mutualisms	Ice cover and ice scour	Relief (slope)
Opportunist and equilibrium species	Segregation of benthic and pelagic realms	Substrate (sediment) particle size
Recruitment mechanisms	Water motions	Basin morphometry (topography)
Migrant species	Convergences and divergences	Geology (rock type)
Larval dispersal	Stratification, mixing regime and nutrients	Substrate heterogeneity
Buoyancy and sinking	Light penetration and turbidity	
Desiccation resistance	Depth and pressure	
Osmotic tolerance	Tidal amplitude and currents	
Spatial and dimensional use	Exposure (to atmosphere and waves)	
Patchiness	Tsunamis, storm surges, hurricanes and water spouts	
Seasonal cycles		
Biological succession		
Human activities		

Fig. 50: Factors determining or correlated with, or controlling the nature and distribution of marine biota (from DAY and ROFF 1999).

A simplified overview of the hierarchical system is given below:

Level 1: Environment Type
Freshwater lotic (streams and rivers), Freshwater lentic (lakes), Estuaries (junctions of fresh and marine waters), Marine (seas and oceans)

Level 2: Geographic Range
Division between the Arctic and Atlantic Oceans based on sea-ice frequency and previously defined extents of the Arctic and Atlantic basins.

Level 3: Temperature
A combination of temperature and sea-ice frequency differentiates also between the Pacific, Atlantic and Arctic Oceans, with further subdivision into definable thermal regimes.

Arctic Waters (avg. temp < 0°C, ice 9–12 months)
Subarctic Waters (avg. temp >0°C ice 6–9 months)
Boreal Waters (avg. temp. > 0°C, ice 1–6 months)
Temperate Waters (avg. temp > 0°C <18°C, ice < 1 month)
Subtropical Waters Subtropical (> 6°C winter, > 18°C summer)

Level 4: Sea-Ice Cover
Permanent Pack Ice, Seasonal Ice, Variable Ice, No Ice, Polynyas

Level 5: Segregation of Pelagic and Benthic Environments

Level 6: Vertical Segregation
Pelagic Realm
Segregate the water column by *depth* intervals at level 6.
Segregate the pelagic zone into *stratified, nonstratified* and *frontal* regions at level 7.

Benthic Realm
Discrimination of community types by depth, which is a correlate for light and pressure.

Pelagic and benthic zones of the ocean:
1 - Nearshore euphotic (0–50 m)
2 - Pelagic euphotic/epipelagic (0–50 m)
3 - Dysphotic/epipelagic (50–200 m)
4 - Aphotic/mesopelagic (200–1000 m)
5 - Aphotic/bathypelagic (1000–2000 m)
6 - Aphotic/abyssal (> 2000 m)

Level 7: Mixing and Wave Action
Pelagic Stratification: The stratification parameter (S) distinguishes regions of the water column that become stratified during the seasonal heating cycle from those that remain vertically mixed. Frontal zones between these two regions are productive areas that represent one type of temperature anomaly. The stratification parameter also describes the broad-scale type of summer nutrient regime: impoverished surface waters in stratified areas versus regions of vertical nutrient replenishment. The stratification parameter also accounts for the effects of tidal amplitude within the pelagic realm. The effects of major ocean currents will already have been accounted for in the distribution of temperature at level 3 of the hierarchy.

stratified (S>2); frontal (1<S<2); nonstratified (S<1)

Benthic Exposure and Slope:

benthic offshore (dysphotic)	*low slope (<1°);*	*high slope (>1°)*
benthic nearshore (euphotic)	*sheltered: fetch < 250 km;*	*exposed: fetch > 250 km*

Level 8: Benthic Substrate
Rock/boulders (incl. bare rock); Pebbles/gravel/coarse sand; Fine sand; Mud/silt

5.1.5 EARLL and FARNHAM (1983)

EARLL and FARNHAM (1983) stressed the continuous character of marine biogeographic patterns. Despite this phenomenon there are boundaries or discontinuities which occur where there is a high frequency of distributional range terminations.

According to these authors, biogeographic provinces should be defined by the proportion of endemic species with endemism rates exceeding 25% beginning to suggest areas where speciation had taken place during evolutionary processes sufficient to warrant the designation as a province. The area around the British Isles was regarded as a transition area, lying to the south of the Boreal province with strong warm temperate influence especially at the western approach and, to a lesser extent, Arctic influences from the north (Figs. 51-53). These patterns were underlined by tables of northern distributional limits of southern faunal elements and southern distributional limits of northern faunal elements. Despite general gradual biogeographic changes along the north-eastern Atlantic coasts a discontinuity of floral distribution patterns between Clare Island and the Faeroes had been emphasised by EARLL and FARNHAM partly on the base of data of VAN DEN HOEK and DONZE (1967).

Different environmental factors (temporal and spatial) have been discussed of which biogeographic variations should be regarded at different geographic scales and biogeographical levels (Fig. 45).

Place	R	C	P	R+C+P	(R+C(/P	R/P	Reference
Newfoundland	55	23	41	119	1.9	1.3	Hooper *et al.* (1980)
Greenland	38	36	68	142	1.1	0.6	Lund (1959)
Iceland	83	54	72	209	1.9	1.1	Caram and Johnson (1972)
Faroes	83	44	73	200	1.7	1.1	Borgesen (1905)
Helgoland, Germany	73	53	56	182	2.2	1.3	Kornmann and Sahling (1977)
Netherlands*	62	58	54	174	2.2	1.1	Den Hartog (1959)
British Isles	334	115	207	656	2.2	1.6	Parke and Dixon (1976)
Ireland	246	87	147	480	2.3	1.7	Guiry (1978)
Roscoff (NW France)	286	96	160	524	2.4	1.8	Feldmann (1954); Feldmann and Magne (1964)
Portugal	246	60	98	404	3.1	2.5	Ardré (1970)
W. Mediterranean	175	40	65	280	3.3	2.7	Coppejans (1980)
Albères (Med.)	259	79	88	426	3.8	2.9	Feldmann (1937)
Canaries	202	69	55	326	4.9	3.7	Borgesen, in Feldmann (1937)
Trinidad	71	38	24	133	4.5	3.0	Richardson (1975)
E. Africa	327	143	97	567	4.9	3.4	G. Lawson (unpublished)
Texas	53	21	14	88	5.3	3.8	Edwards (1970)
Jamaica	161	123	47	331	6.0	3.4	Chapman (1961, 1963)

* Indigenous and drift species.

	$(R+C)/P$	R/P
Arctic	2	1.5
Cold temp.	2–3	1.5–3
Warm temp.	3–5	3–4
Tropical	5	4

Fig. 51 left and Fig. 52 above: Ratios of red (R), green (C), and brown (P) algae in the North-East Atlantic used for the delimitation of provinces. These floristic characteristics are based on the higher dominance of brown algae in colder waters and the higher preponderance of red and green algae in warmer waters (from EARLL and FARNHAM 1983).

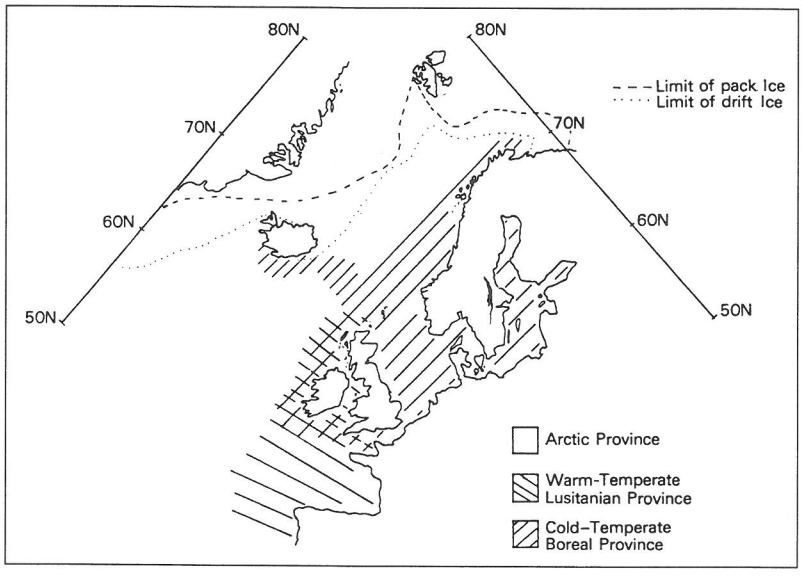


Fig. 53: The biogeographical provinces of the North-East Atlantic based on the classification of BRIGGS (1974) (from EARLL and FARNHAM (1983).

5.1.6 Hayden, Ray, and Dolan (1984): *Classification of Coastal and Marine Environments*

This classification, combines the faunal provinces of Briggs (1974) with physiographic features divided into ocean realms (currents) and coastal realms. It was prepared for the IUCN for nature protection purposes.

Dietrich's (1963) classification of oceanic regions was merged with annual average atmospheric circulations to get a system of natural oceanic regions but only for surface waters.

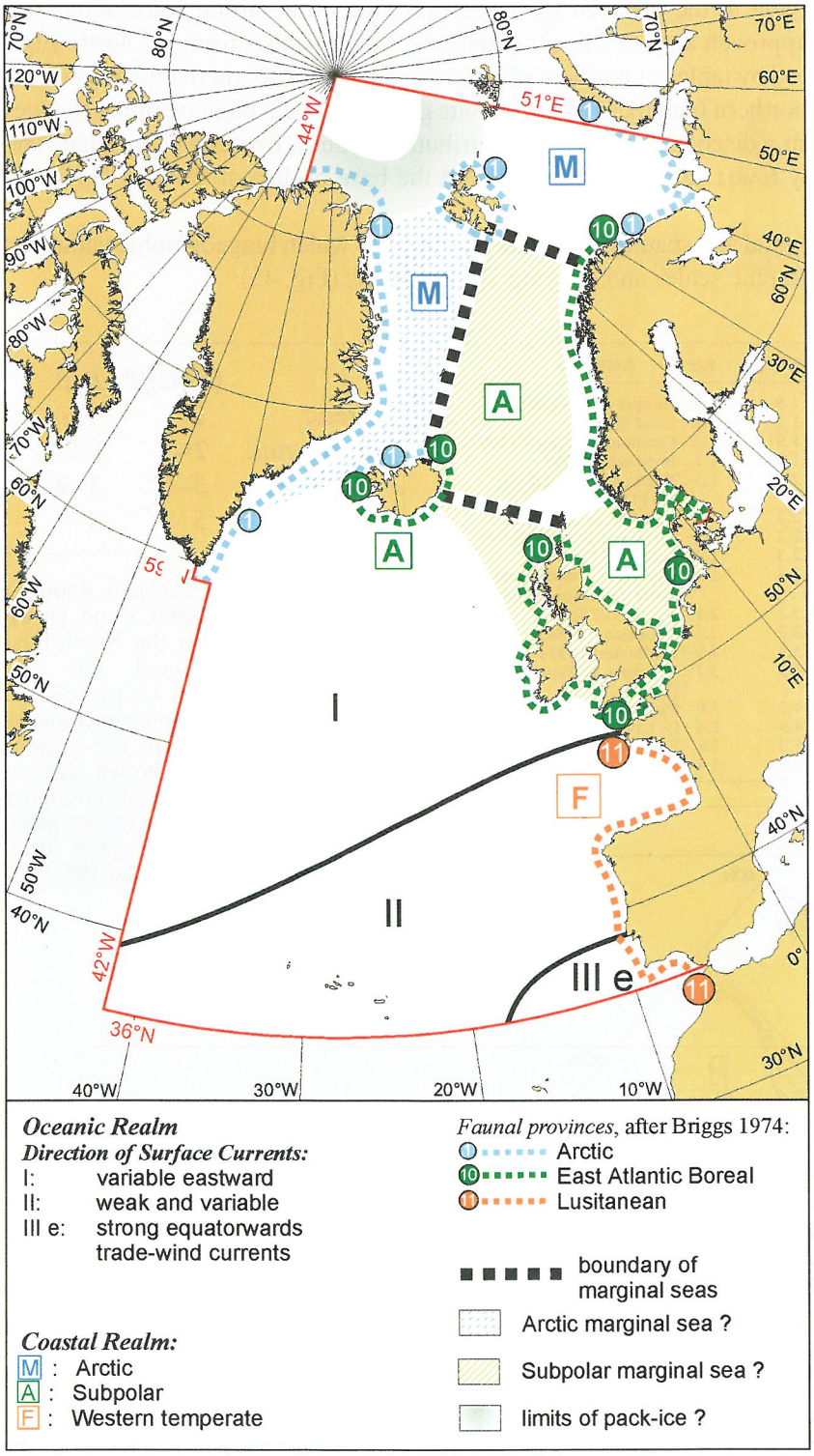


Fig. 54 Classification of Coastal and Marine Environments (from Hayden et al. 1984, redrawn).

Although Briggs' (1974) classification had been followed closely for the zoogeographical part of the classification, oceanic island had been fallen biogeographically into oblivion.
For coastal realms currents, windstreams, coastal geomorphology, temperature and salinity were considered. These coastal realms were assumed to coincide with the boundaries of biotic provinces.

Marginal seas are situated between coastal margins and continents or between two coastal margins and are classified according to the adjacent coastal realm they are associated with.

The result is a two-dimensional classification with the following fundamental biomes: open oceans, coastal margins, marginal seas, and marginal archipelagos.

Furthermore the authors suggested the development of matrices which cross-reference provinces with habitats to ensure that all habitat types are included within representative protected areas.
They also emphasised a further development of the third vertical dimension and the fact that it would be equally important to align marine vegetation patterns to this system.

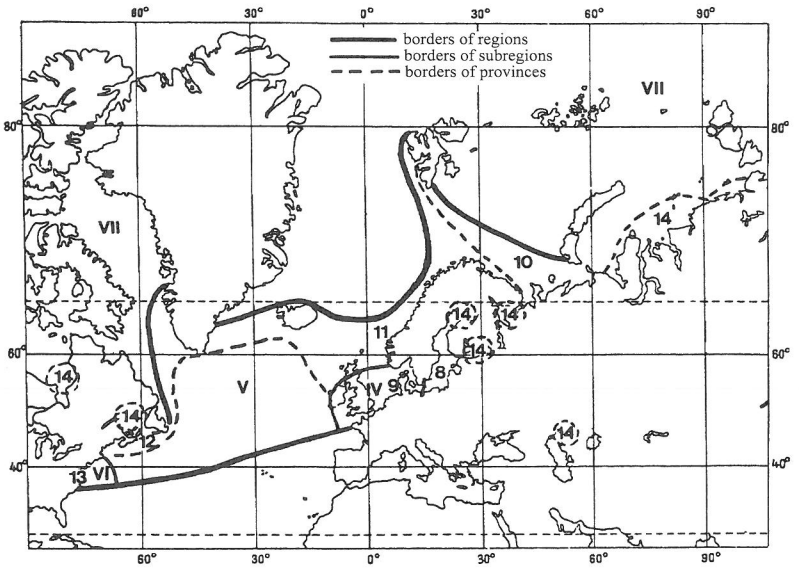
5.1.7 Golikov, Dolgolenko, Maximovich, and Scarlato (1990)

According to these authors this interrelated landscape and flora-faunistic approach is based to a great extent on the analysis of the modern distribution of qualitative composition and quantitative development of species populations and higher taxa applied to the three principles of biogeography: provinciality, zonality, and history.

Golikov et al. emphasised the role of age and place of origin of the different floras and faunas with succession and sources of formation in different world regions, different latitudes, and different depths.
Ecophysiological adaptations should have been related to species level, while morpho-functional adaptations became distinct during the emergence of higher taxa. Physical and chemical environment changes preceded speciation and caused emergence of new species related to the formation of certain water masses. Therefore, as a result, species of each biogeographical group are associated in their distribution with definite water masses comprising a hydrobiocomplex.

Genetical sources from where distribution, adaptation, and speciation had taken place should have spread with the longest time for evolution from tropical regions to temperate and even cold regions. The Arctic region being the youngest biogeographic formation in terms of hydrological and biological appearance is mostly under control of North Atlantic waters but with most inhabitants being of Pacific origin.

The hierarchical system of a landscape-geographical approach, integrating bio-ecological elements into landscape divisions, was analysed in the second part of this classification. In rising hierarchical levels these elements in landscape divisions are: Individual → Monocene + Monotope → Population → Democene + Ecotope → Biocenosis → Ecosystem → Association → Facia → Biome → Formation. Subdistricts appear to be the first flora-faunistic biogeographical divisions. Districts are characterised by the presence of original intraspecific forms. Endemics on species level are peculiar to provinces, genera to subregions, which frequently have endemic families, super-regions may contain original orders, while kingdoms include even whole classes.



Tropic kingdom
II Caribbean tropical subregion
III Mediterranean-Lusitanic subtropical subregion

Temperate/Cold kingdom
Atlantic boreal region
IV Celtic low boreal subregion
8 Baltic province
9 North Sea province
V Norwegian high-boreal subregion
10 Barents Sea province
11 Scandinavian province

Arctic region
VI Virginian low boreal subregion
13 Virginian province
VII Eurasian subregion
14 Estuary-Arctic interzonal province

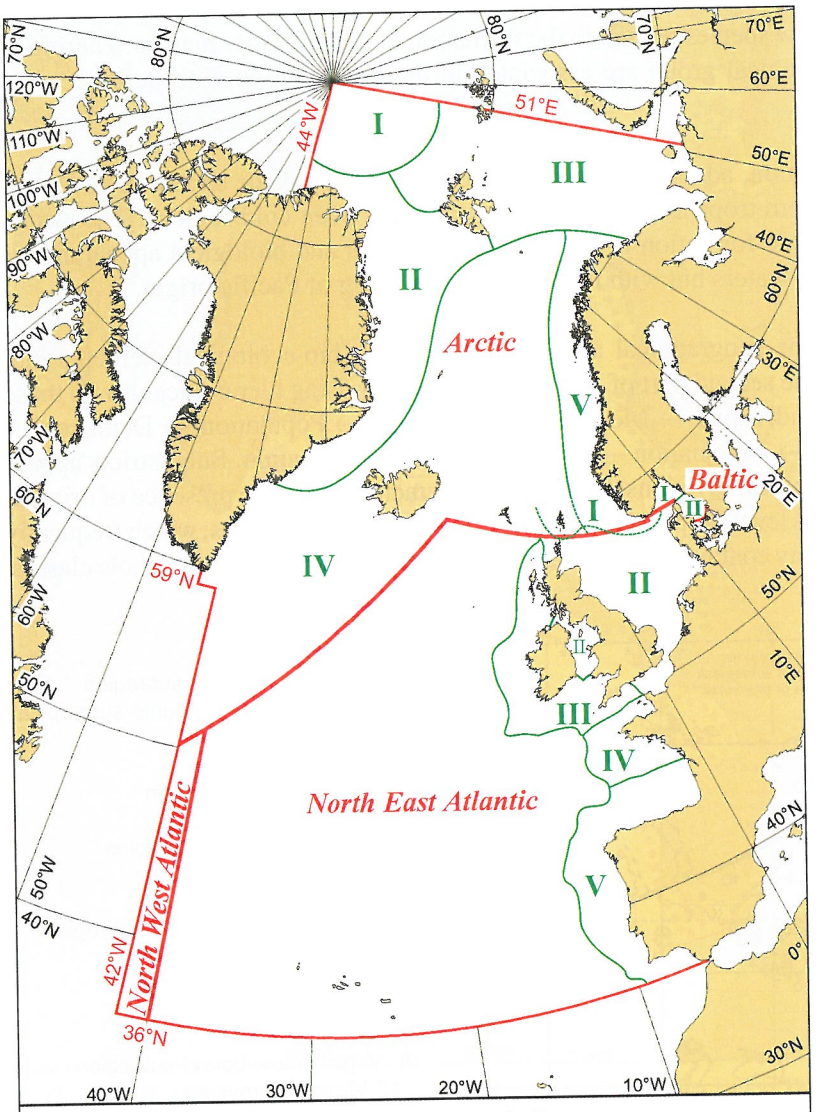
Fig. 55: Biogeographical division of the kingdom of temperate and cold waters of the northern hemisphere on flora-faunistic genetical basis (from Golikov et al. 1990, modified).

5.1.8 Great Barrier Reef Marine Park Authority, The World Bank, IUCN-CNPPA (1995): *A Global Representative System of Marine Protected Areas*

Arctic: Bleakley and Alexander; Northeast Atlantic: Gubbay

(Baltic: Esping and Grönqvist; North West Atlantic: Mondor, Mercier, Croom and Wolotira)

This heterogeneous classification has been used by different authors to describe biogeographically representative regions and zones in which a system of MPAs should be established. The presence of rare biogeographic qualities or representative of a biogeographic "type" were named as the first criteria for the selection of priority areas for conservation.



CNPPA Marine Regions and **Biogeographic Zones**

Arctic:
- I High Arctic Oceanic
- II High Arctic Coastal
- III Arctic Coastal
- IV Arctic Maritime
- V Norwegian Coast

Baltic:
- I Skagerrak
- II Kattegat

(North West Atlantic)

North East Atlantic:
- I Boreal-Arctic
- II Boreal
- III Boreal-Lusitanean
- IV Lusitanean-Boreal
- V Lusitanean

Comment:
Indistinct boundaries around the area between south Norway and the Shetland Islands might be due to incompabilities in the designation of the different authors.

Large parts of the Arctic and the NEA classification have been integrated in this map presenting the OSPAR area while parts of the Baltic (Skagerrak, Kattegat) and the NWA are covered only marginally.

The Arctic has been subdivided into the High Arctic that experience permanent pack ice and low productivity with life cycles adapted to very strict timetables.
Subarctic areas, with their extraordinary high productivity and biomass, are in striking contrast to the Arctic. Further subdivisions were made due to oceanic character versus coastal margin realms.

The whole of Norway with its character of a double (S-N, O-W) biogeographic gradient and which has a complete boreal nature was incorporated into the Arctic marine region for practical purposes.

The North-East Atlantic region was divided into northern Boreal and southerly Lusitanean subregions with further subdivisions that indicate the continuous character of change in faunal and floral distribution.
The Azores (and Madeira) depict a separate biogeographic zone even though not marked on the map.

Fig. 56: CNPPA Marine Regions and Biogeographic Zones (from Kelleher et al. 1995, redrawn).

5.1.9 Hiscock (1998): *Biogeography of the North-East Atlantic*

This biogeographic scheme is presented in an extensive work about "Benthic marine ecosystems of Great Britain and the north-east Atlantic" which was largely based on benthic classifications of communities and habitats of the BioMar-project/JNCC-MNCRs (UK and Ireland).
The classification itself is based on a review of diverse sources and earlier works of different biogeographers and thus delimitations of the different coastal benthic units are rather similar to the one developed in this study.

The seas around Great Britain are regarded as being centred in the Boreal region despite a great range of different physical and chemical conditions.
Although many biogeographical changes are considered to occur gradually over large distances, the seas in this area include boreal-arctic and especially at the south-western approach boreal-lusitanean characteristics, thus leading to a great variety in marine biodiversity.

A marked biogeographic change on the northern coast of Spain has been described but without further consideration in the map.

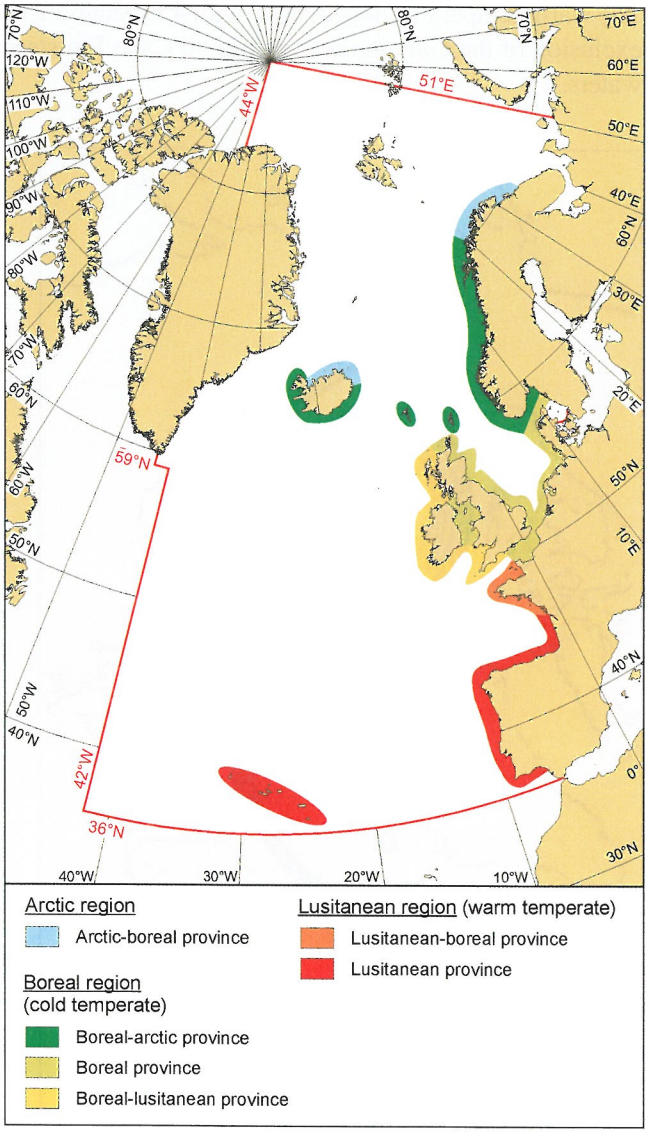


Fig. 57: Biogeography of the North-East Atlantic (from Hiscock 1998, redrawn).

Comment: Shown classified areas are incomplete to the north and south due to a different cartografical projection.

5.1.10 Glémarec 1968/1998/2000

The NE-Atlantic was divided on the basis of the distribution of bivalves at a species level into Cold (Arctic), Cool, Mild, and Warm Temperate subprovinces being covered by the OSPAR area (Fig. 60) with further consideration of a Subarctic/Arctic-Boreal subprovince north of the Lofoten Islands.
Glémarec identified 22 bivalves of true Arctic character within the group of cold origin in the OSPAR area. Another 65 species of an Arctic-Boreal group of which 2/3rd are of amphiatlantic character are penetrating southward by submergence into bathyal étages as far as the Bay of Biscay (Fig. 58).
The bivalves group of warm origin, which might have survived in bathyal depths during the Pleistocene, consist of 173 species (Fig. 59).

The 61 most eurythermal species have a distribution range from Gibraltar to the Lofoten. A cool temperate subprovince between 64° and 68° northern latitude is marked by a nearly equal presence of cool temperate and arctico-boreal species. Another 36 cool temperate species reach along the Finnmark coast, which might be declared as a subarctic subprovince.
A mild temperate subprovince covers the area from St Jean de Luz (Gulf of Gascony) to the Trondheim Fjord (Norway, 64°N) and can be further subdivided due to northern limits of species of warm origin: 6 species as far as Brest/Brittany; 14 species to the western Channel, Irish Sea and western Ireland; 7 species to the Orkney-Shetland channel; 17 species to the southern North Sea and 26 species as far as Trondheim. Being a region of transition there is also a rich proportion submerged arctico-boreal species.
The warm temperate subprovince, with 42 species of warm origin, stretches along the Iberian coasts with the exclusion of the Galician region around Cape Finisterre with its mild temperate character due to upwelling waters.

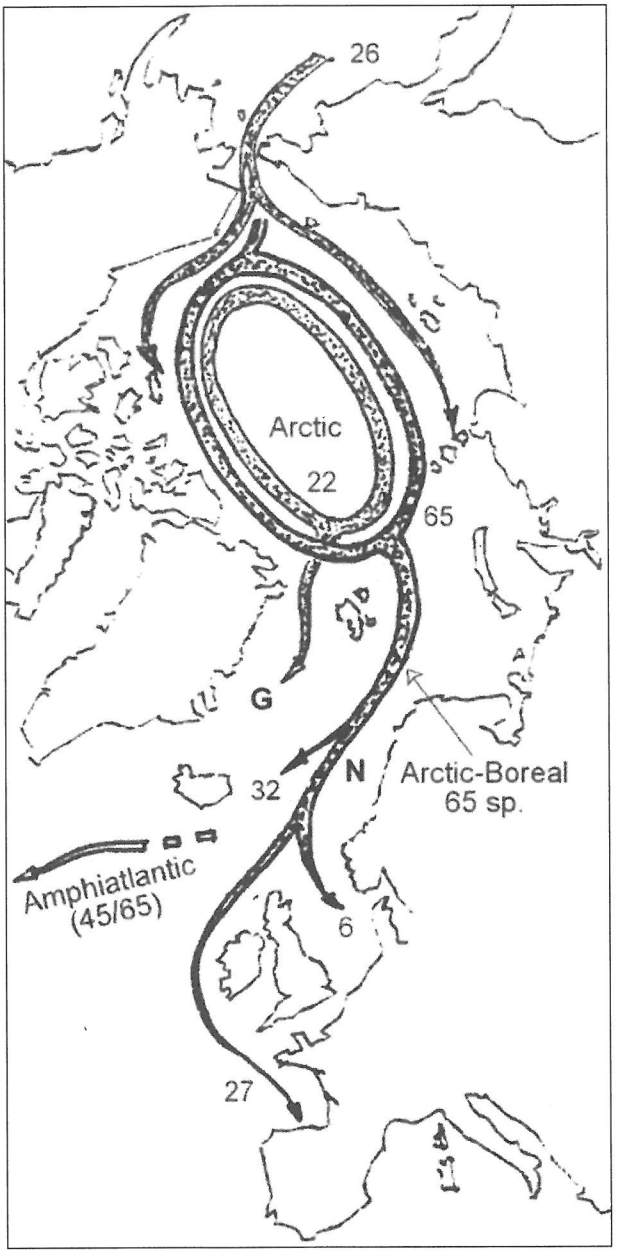


Fig. 58: Bivalves of the NEA of cold origin (from GLÉMAREC 1998).

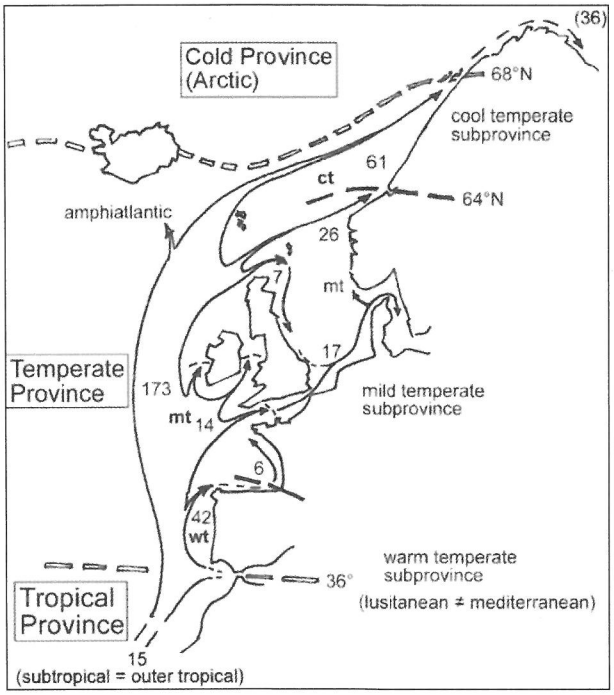


Fig. 59: Bivalves of the NEA of warm origin (from GLÉMAREC 1998, modified 2000).

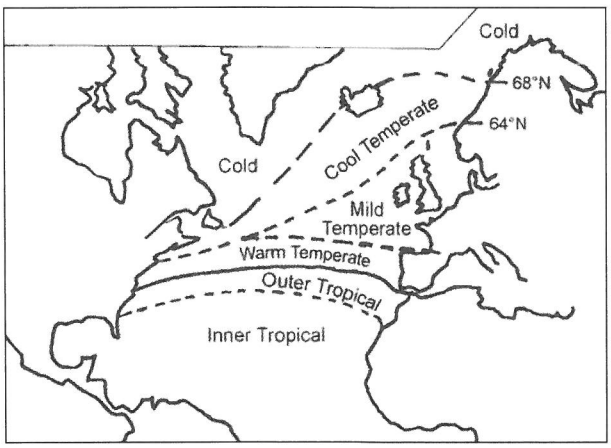


Fig. 60: Atlantic provinces and subprovinces based on bivalve distribution limits (from GLÉMAREC 1998).

5.1.11 Backus, Cradock, Haedrich, and Robinson (1977): *Atlantic Mesopelagic Zoogeography*

On the base of 1,022 midwater trawls, mostly at depths from 240-800 m at day and < 200 m at night and collections from 531 neuston stations in the Atlantic between ~ 65°N and 40°S, a system of mesopelagic zoogeographical regions, provinces, and distribution patterns had been discriminated by Backus et al. (1977) and Backus (1986) with data of mesopelagic fish records and boundary delimitations given by Backus and Cradock (1977a, b).

Fish data, having been collected mostly on transects, were examined for faunal change. Locations along the transects of marked faunal change were examined for evidence of physical change. The physical change was assumed always to exist and was generally readily detectable in the presence of a marked faunal change, with which it was assumed to be directly related. Such physical changes were related to and identified with some widespread oceanographic circulational feature. Furthermore this circulational feature was plotted with the use of physical oceanography and thus was taken as the faunal boundary.

Using this procedure an "Atlantic Subarctic" region and a "North Atlantic Temperate" region, later subdivided into the "Northern Gyre", "Azores-Britain", "Mediterranean Outflow" provinces, were identified for the OSPAR area (Fig. 61). The "North Atlantic Subtropical" region with its "Northern North African Subtropical Sea" province is touched only marginal. The Subarctic region is characterised by its very low diversity and the myctophid species living there which also occur in the adjacent temperate seas. The Arctic was not thought likely to contain a mesopelagic fish fauna although Backus (1986) published a more generalised biogeographic map including the Arctic with a delimitation against the Atlantic Subarctic based on Dunbar (1951).

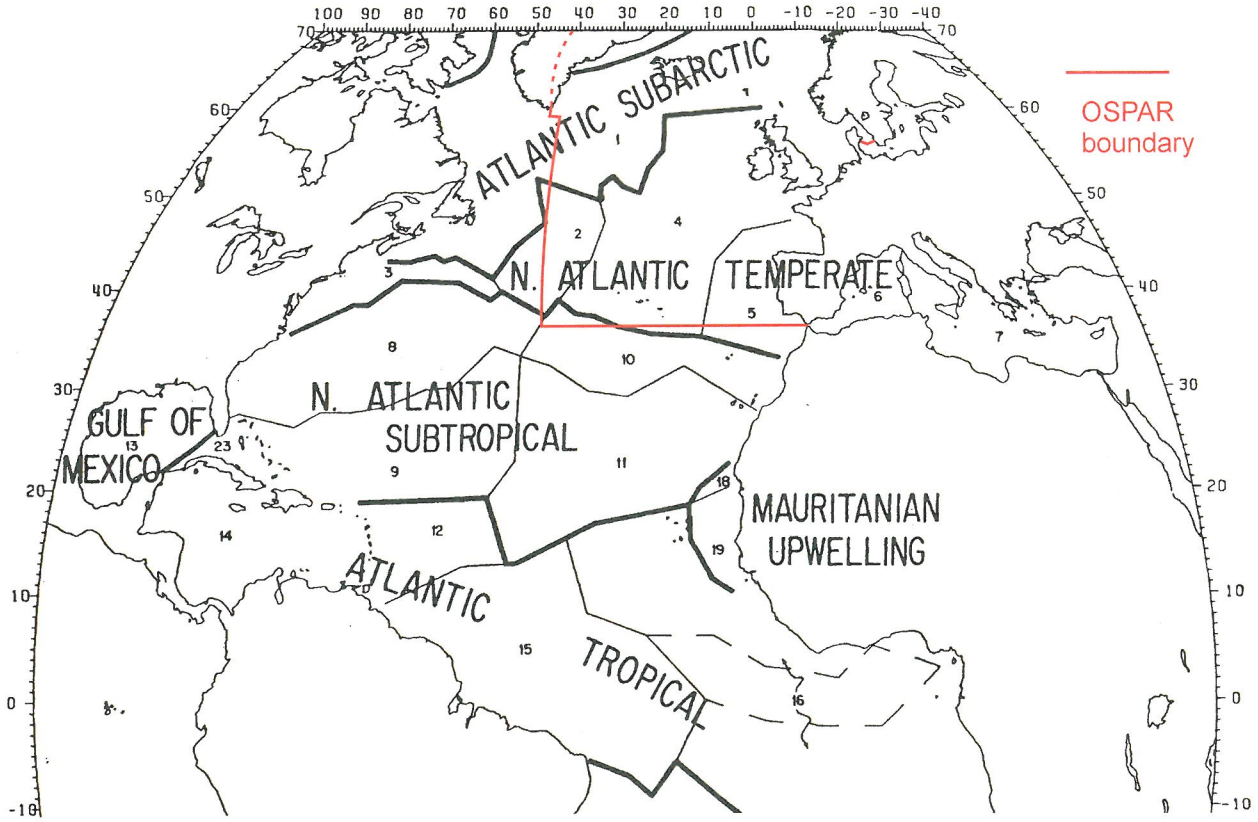


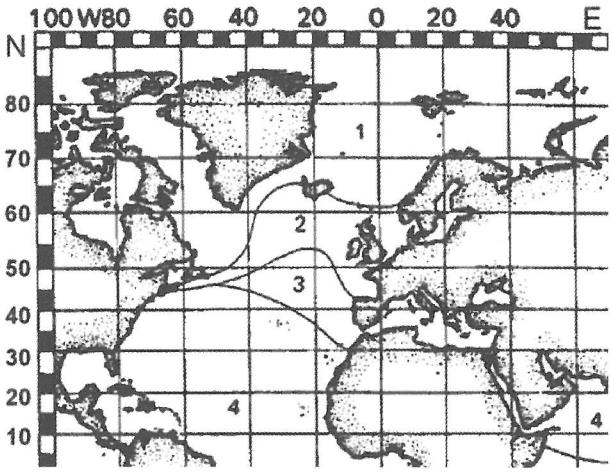
Fig. 61: Mesopelagic ichtyogeographic classification (from Backus, Cradock, Haedrich, and Robinson 1977; clipped and OSPAR boundary added): The heavy lines set apart the regions, the light lines the provinces according to the following numbers: 1. Atlantic Subarctic; 2. Northern Gyre; 4. Azores-Britain; 5. Mediterranean Outflow; 10. Northern North African Subtropical Sea;

5.1.12 VAN DER SPOEL and HEYMAN (1983): *A Comparative Atlas of Zooplankton*

This Atlas contains a remarkable extensive selection of maps dealing with pelagic biogeography. Only few examples can be presented here.

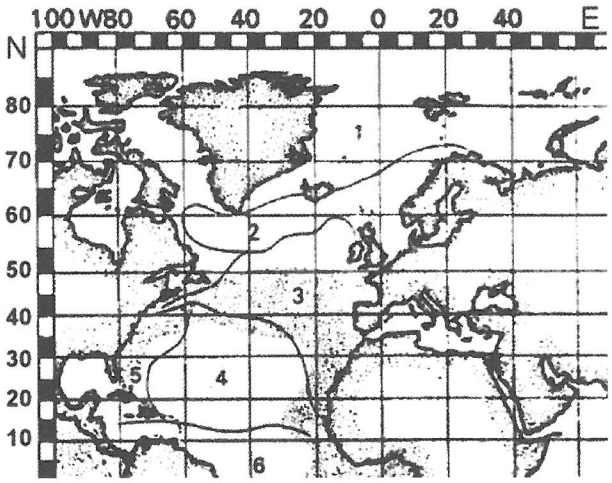
Showing dominantly zooplankton (*e.g.* Fig. 62), but also phytoplankton (Fig. 63), ichtyoplankton, and vertebrate patterns (fishes excluded), meso- and bathypelagic patterns, and maps of oceanographic features, resulting general biogeographic pattern (Fig. 64), the following pelagic patterns were distinguished:

- beltshaped patterns latitudinal wide ranging and partly with species submergence;
- beltshaped patterns with warm-water ranges and cold-water ranges;
- oceanic or central-water with cold-water and tropical patterns;
- not-beltshaped oceanic patterns;
- endemic patterns;
- neritic patterns with warm-water patterns and cold-water ranges;
- distant-neritic patterns;
- disjunct or continuous distributions;
- different types of speciation;
- different types of allopatric abundance;
- different types of sympatric abundance;
- distributions grouped around a faunal centre.



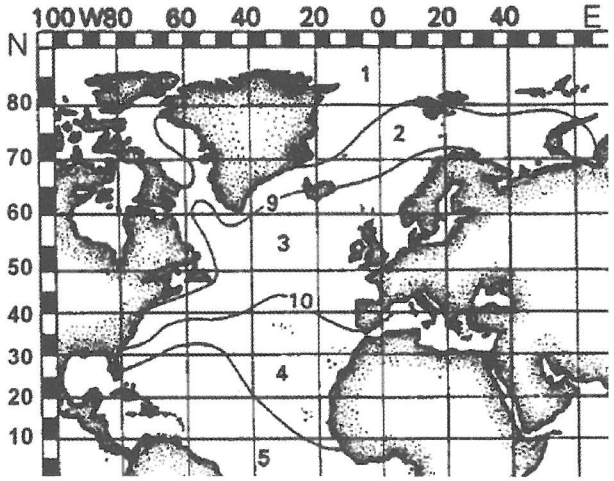
1 = Arctic area
2 = Arctic-Boreal area
3 = Northern Transitional area
4 = Tropical area

Fig. 63: Phytoplankton geography (from VAN DER SPOEL and HEYMAN 1983; clipped).



1 = Arctic area
2 = Subarctic area
3 = Northern Temperate area
4 = Northern Subtropical area
5 = Northern Subtropical-Terminal area
6 = Equatorial area
dotted = areas of strong mixing water masses

Fig. 62: Zooplankton geography (from VAN DER SPOEL and HEYMAN 1983; clipped).



1 = Arctic zone
2 = Subarctic zone
3 = Cool-Temperate zone
4 = Warm-Temperate zone
5 = Tropical zone
9 = Dunbar line (5°C average isotherm)
10 = Ortmann line (15°C average isotherm)

Fig. 64: Pelagic biogeographic zones (from VAN DER SPOEL and HEYMAN 1983; clipped).

5.1.13 LONGHURST (1998): *Ecological Geography*

Focussing his work on pelagic surface production patterns, Longhurst evaluated mainly phytoplankton chlorophyll distribution and density data gained from Coastal Zone Colour Scanner (CZCS) images of the NIMBUS satellite system.
These and other oceanographic data sets, such as sea surface temperatures, were obtained in short time intervals for several years, and assessed with regard to plankton productivity patterns with a view to predicting dependent biological patterns.

Polar, Westerly Winds, Trade Winds (= Tropical), and Coastal Boundary biomes were differentiated because of the different processes leading to dependent characters of mixing and layering (Longhurst 1995). Biome zones were characterised by a quantification of taxonomic and aggregated trophic plankton groups in percentage of carbon biomass. These biomes are delimited by frontal boundaries and contain various provinces distinguished by different patterns of productivity. Three major provinces were incorporated in the Polar biome because of their similar characteristics. But it was stated that the geographical limits might change seasonally even far beyond the polar fronts. The Westerlies biome was regarded as a transition between the Polar and Trade Wind biomes, showing characteristics of each. The Coastal Boundary biome shows much more diversity in its patterns due to a wide temperature range and seasonality, with patterns being formed by the interaction of oceanic circulation, tides, and continental topography.

Longhurst criticised classical marine biogeography amongst other things for its lack in methodology, for insufficiencies related to difficulties in plankton taxonomy due to common phenotypic variations, and vaguenesses related to species emergence ↔ submergence, and expatriation.
On the other hand this approach did not give any descriptions of shallow and deep benthic and bathypelagic ecology.

Also patterns of the neritic coastal fringe shoreward of the coastal turbidity fronts, occurring along almost all coasts, could not be handled by the evaluation of satellite images.

Longhurst further suggested the use of such ecological geography as a framework for systematical biogeography as a fill-in, as far as taxonomic patterns are known.

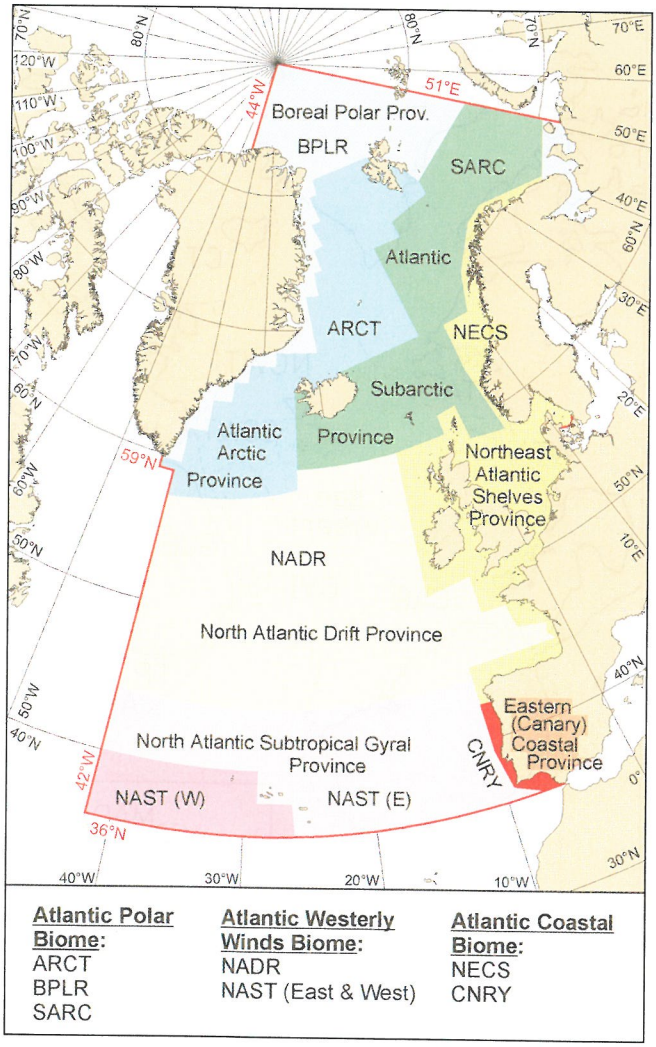


Fig. 65: Ecological geography (from LONGHURST 1998, redrawn).

5.1.14 Prud'homme van Reine and van den Hoek (1990): *Biogeography of Macaronesian Seaweeds*

Partly integrating former publications (Prud'Homme van Reine 1988; Prud'Homme van Reine and van den Hoek 1988) and data about the seaweed biogeography of the Macaronesian mid-Atlantic islands, these authors statistically identified a Macaronesian biogeographic seaweed region *in sensu strictu* comprising the Madeira, Canary (L/F and OC groups), and Salvage islands and archipelagos (Fig. 66). These four island groups were closely related to the Western Mediterranean region with imprints from eastern America (largely Caribbean) that make them distinct from the subtropical West-African flora. This could be due to a similar temperature regime or due to currents (Fig. 15) and possibly thereby implied dispersal patterns. In contrast to this, the Azores were only related to the Macaronesian region in a wider sense with their impoverished flora even closer related to species of amphiatlantic distribution. Only 189 seaweed species have been recorded for the Azores with 10 of those as being endemic (Prud'Homme van Reine 1988). Affinities of theses "chance survivors of chance invasions" were partly closer to the WM, NCWT, and SCWT regions than to other Macaronesian groups. The boundary between the Ct and NCWT regions in this classification roughly corresponds with the discontinuity described by Earll and Farnham (1983) and van den Hoek and Donze (1967), while the boundaries between the NCWT, SCWT, and subtropical West-African regions depict further subdivisions of the former Lusitanean province of the warm-temperate Mediterranean-Atlantic region of van den Hoek (1975) (Chap. 5.1.16).

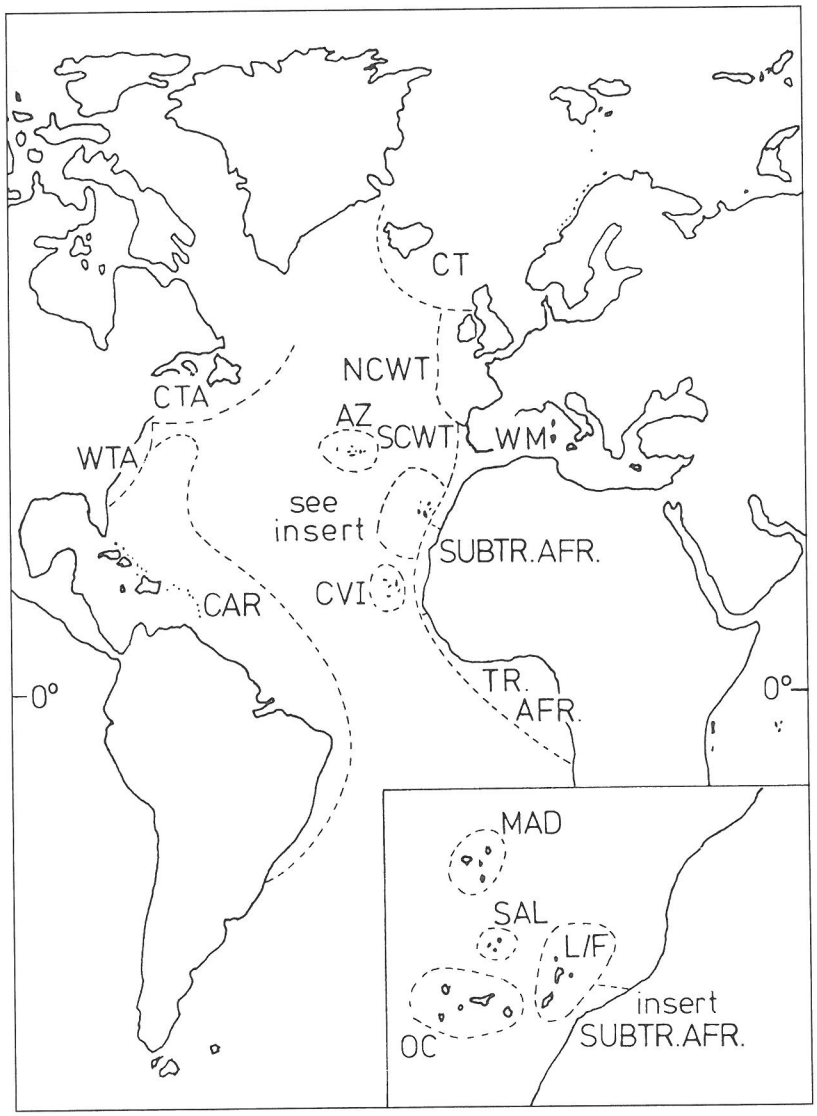


Fig. 66: Biogeography of Macaronesian Seaweeds (from Prud'homme van Reine and van den Hoek 1990):

AZ	Azores
CAN	Canary Islands (OC and L/F together)
CAR	Caribbean
CT	Europe: Scotland, Norway, North Sea and Baltic
CTA	NE America, north of Cape Cod
CVI	Cape Verde Islands
L/F	Lanzarote, Fuerteventura and surrounding islets
MAD	Madeira Archipelago
Macar. s.s.	Macaronesia sensu strictu (L/F, MAD, OC, and SAL)
NCWT	NE Spain, Atlantic France, S, SW, and NW England, Wales, Ireland (Northern cooler warm temperate areas)
OC	Canary Islands except L/F
SAL	Salvage Islands
SCWT	Morocco (excl. former Spanish Sahara), Atlantic SW Spain, Portugal (Southern cooler warm temperate areas)
Subtr. Afr.	NW Senegal (North of Gambia), Mauretania, former Spanish Sahara
Tr. Afr.	From Gambia to Congo Rivers
WM	Western Mediterranean
WTA	NE America between Cape Canaveral and Cape Cod

5.1.15 Lloris, Rucabado, and Figueroa (1991): *Biogeography of the Macaronesian Ichtyofauna*

An inventory of 913 fish species (102 chondrichtyes and 811 osteichtyes) of the Macaronesian region was examined for geographical provenience and relationships between the species. A similarity analysis between the archipelagos Azores, Madeira, Canaries, Cape Verde, and an African Site – neighbouring the Canaries and adjacent areas to the south – gave affinities in shared species according to figure 67, which were also attested by the statistical analysis of genera and families.

Of the whole Macaronesian region 16.4% of the species were identified to belong to the Atlanto-Mediterranean group, 13.4% were endemics with a centre around Madeira, 11.9% were Amphiatlantic species, 7.3% were Cosmopolitan species, 6.8% were Boreal species, 24.9% were assigned to Equato-Guinean origin, and 24.2% were Circumglobal species.

Analysing families, the Azores showed a closer affinity to Madeira within the Macaronesian archipelagos, but they were quite isolated on generic and even more on species level.

Overall the Macaronesian region was regarded as an ichtyofaunistic crossroad (Fig. 68). There was a high degree (43.4%) of Amphiatlantic, Circumglobal, and Cosmopolitan species merging with a "septentrional/ northern" group (Boreal, Atlanto-Mediterranean, Endemics) of 27.2%, and the southern Equato-Guinean group (29.4%), with the latter two groups give the Macaronesian region its predominant character but without being a biogeographical unit in its own right. The resulting hierarchical ranking is shown in figure 69.

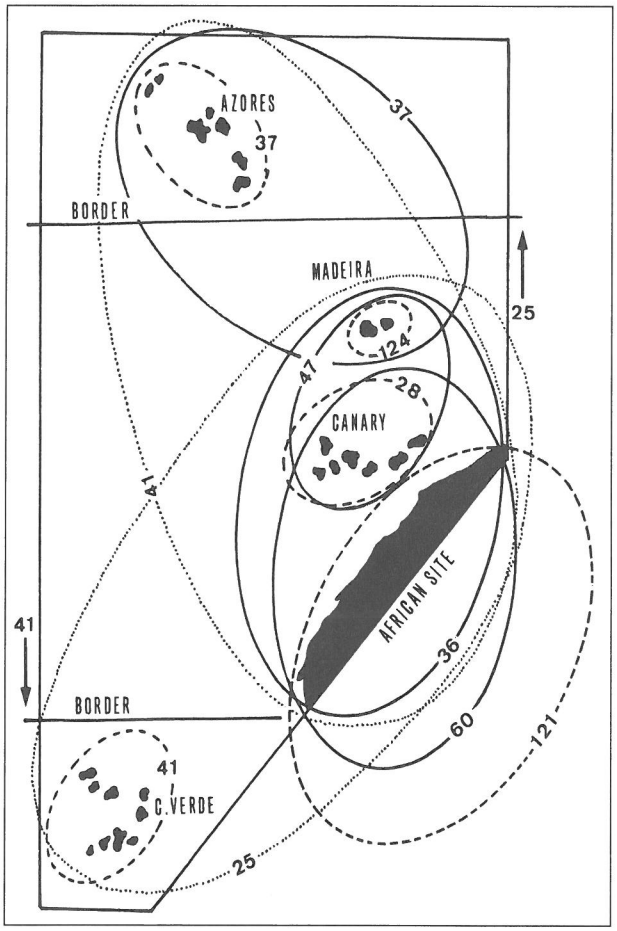


Fig. 67: Exclusive and most relevant species groups of and between the different Macaronesian geographic units. To note, the northern group (41 species), common to all localities except the Cape Verde islands, is composed mainly by equatorial species (46%) (from Lloris et al. 1991).

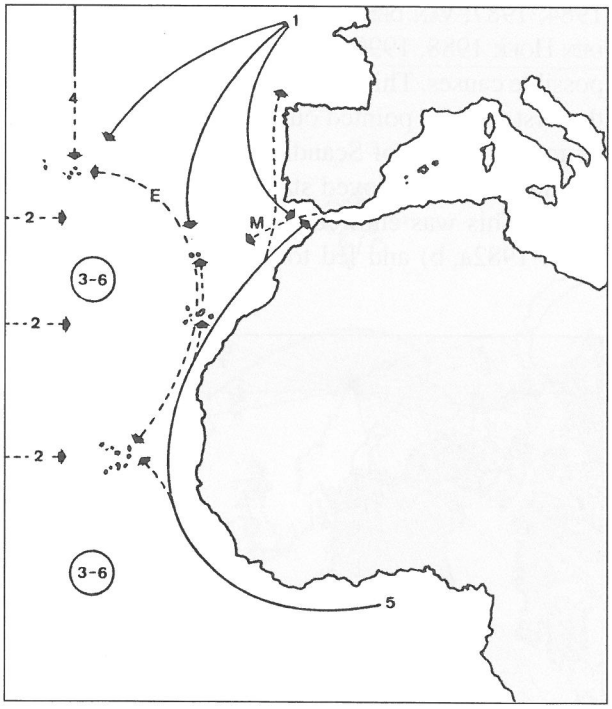


Fig. 68: Distribution model for the Macaronesian region as being an ichtyofaunistic transition area (Continuous trace is used for dominant faunae) (from Lloris et al. 1991):
1 and M: Atlanto-Mediterranean;
2: Amphiatlantic;
3-6: Circumglobal and Cosmopolite;
4: Boreal;
5: Equato-Guinean
E: Endemic

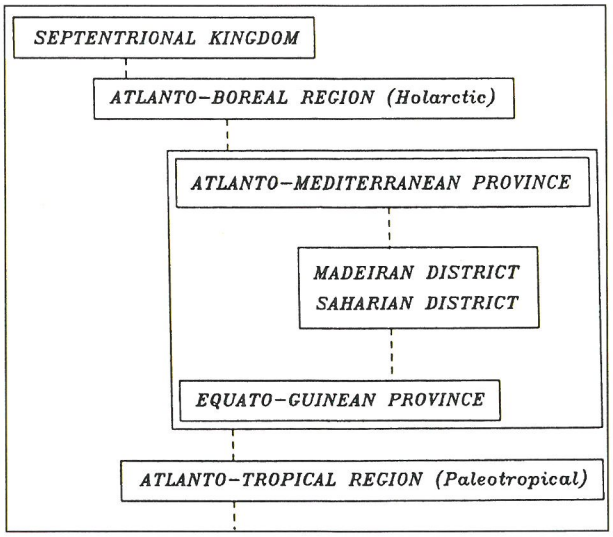
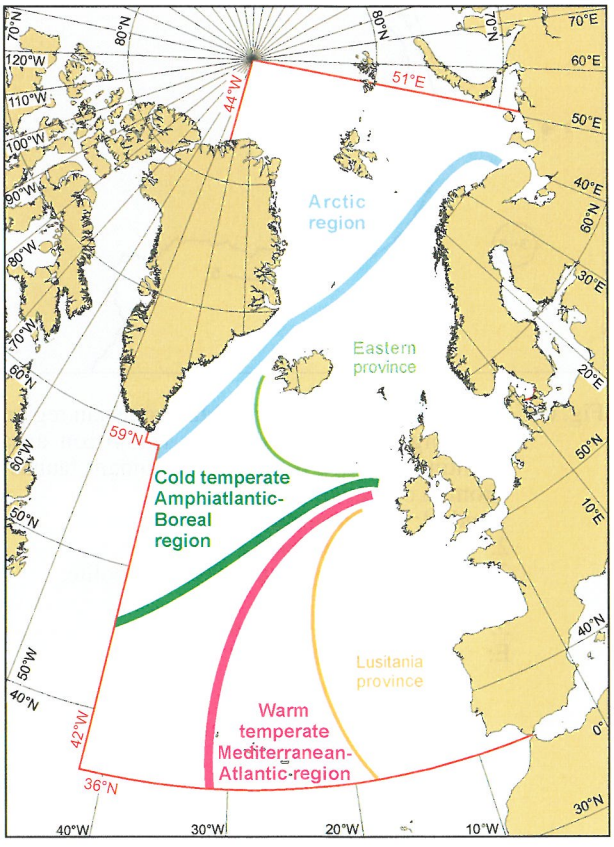


Fig. 69: Hierarchical proposal of biogeographic levels for the studied area (from LLORIS et al. 1991).

5.1.16 VAN DEN HOEK (1975): *Phytogeographic (Seaweed) regions and provinces*

In series of publications (as VAN DEN HOEK and DONZE 1966, 1967; VAN DEN HOEK 1975; 1979; 1982a, b, c; 1984; 1987; VAN DEN HOEK and BREEMAN 1989; VAN DEN HOEK et al. 1990; PRUD'HOMME VAN REINE and VAN DEN HOEK 1988, 1990) VAN DEN HOEK dealt with distribution patterns of seaweeds in the North Atlantic and possible causes. This was based on a survey of algal phytogeography along the European Atlantic coasts. For the first time he pointed out that the discontinuities between the cold Arctic waters of Spitzbergen and cold temperate waters of Scandinavia and between cold and warm temperate waters at around Clare Island/W-Ireland could be proved statistically, correlated with surface temperatures, and (VAN DEN HOEK and DONZE 1967). This was enforced by laboratory experiments about the ecological amplitude of species (VAN DEN HOEK 1982a, b) and led to this phytogeographic classification. The boundaries were mainly confined to surface isotherms with the Amphiatlantic-Boreal region lying between the 10°C summer-isotherm to the Arctic and the 10° winter- or 15° summer-isotherm to the warm temperate Mediterranean-Atlantic region (VAN DEN HOEK 1975).



For the OSPAR area, VAN DEN HOEK (1982a) further identified the following distribution groups, including key species, with the help of the recognition of southern/warm and northern/cold lethal, growth, reproduction, and complex boundaries:

- Arctic group
- Amphiatlantic temperate group
- Amphiatlantic temperate group with a southern boundary near a summer isotherm
- Amphiatlantic temperate group with a southern boundary near a winter isotherm
- Amphiatlantic tropical-to-temperate group
- Amphiatlantic tropical-to-temperate group with northeastern extension
- Amphiatlantic tropical-to-temperate group with northwestern extension
- Warm temperate Mediterranean-Atlantic group

Fig. 70: Phytogeographic (seaweed) regions and provinces (from VAN DEN HOEK 1975; redrawn).

5.1.17 Lüning (1985): *Marine Botany*

In his book about marine botany Lüning (1985) gave detailed descriptions of seaweed ecology, distribution, physiology, and human use with a focus on the North Atlantic.

Reflecting isotherms as being the most decisive factor for marine distribution patterns his classification is closely related to the biogeographic schemes of Briggs (1974) and Michanek (1979).

For the North Atlantic the isotherms used are the 10°C summer and 0°C winter isotherm to delineate between the Arctic and the cold temperate regions, and the 15°C summer and 10°C winter isotherm between the cold temperate and warm temperate regions. This approach is broad and should be modified to take account of peculiarities of the different coastlines and substrates. They do however coincide with temperature boundaries of many seaweed groups *e.g.* they are exact for laminariales which follow the 20°C summer isotherm in their southern distribution limits.

This author also assumes the existence of northern (corresponding to the winter isotherm) and southern (corresponding to the summer isotherm) lethal, reproduction, growth, or complex boundaries for seaweeds given by van den Hoek (1982a, b) with regard to the northern hemisphere.

The Subarctic region of Børgesen & Jónsson (1905/ 1908) and Michanek (1979, 1983) has been incorporated into the Arctic region of Lüning (1985) because there are no Subarctic endemic seaweeds and such a delineation seemed to be difficult due to a indistinct delimitation from northern boundaries of cold temperate seaweeds.

Lüning gives a boundary between the cold temperate and the warm temperate region at west Ireland and the western Channel.

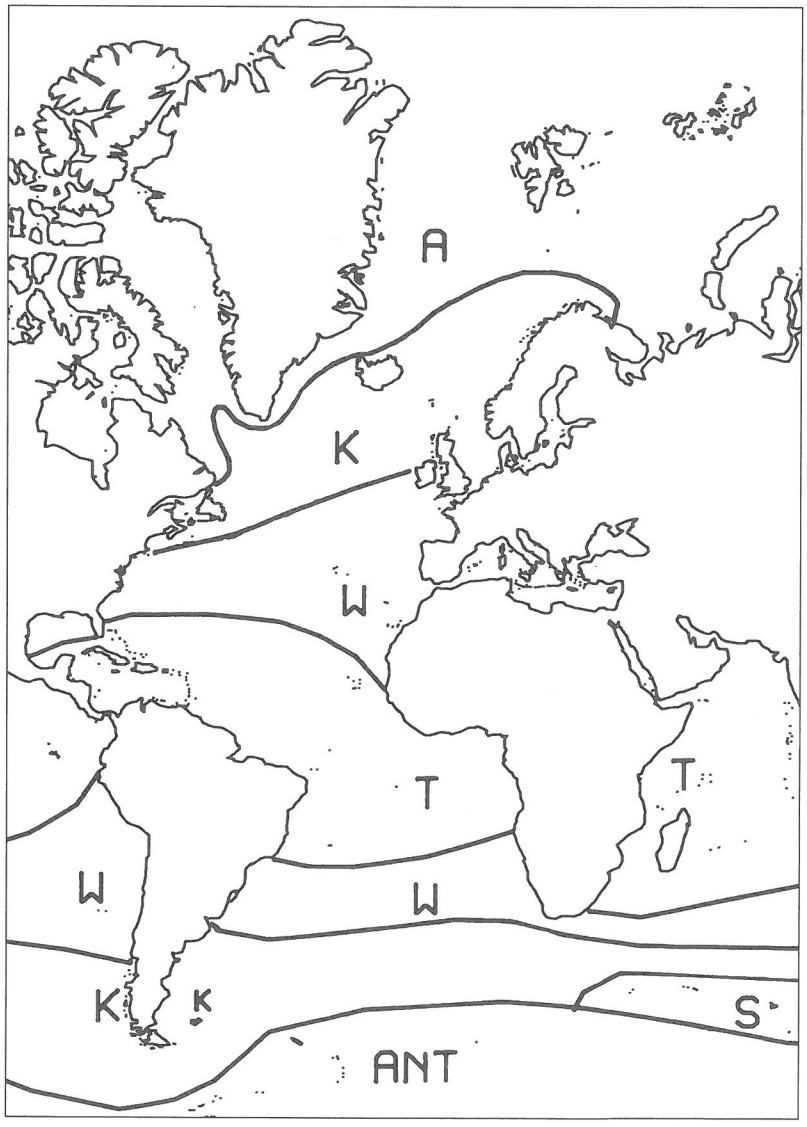


Fig. 71: Groups of marine biogeographic regions (from Lüning 1985):
A: Arctic region
K: Cold temperate region
W: Warm temperate region
T: Tropical region
S: Subantarctic Island region
Ant: Antarctic region

5.1.18 Alvarez, Gallardo, Ribera, and Garreta (1988): *A reassessment of Northern Atlantic seaweed biogeography*

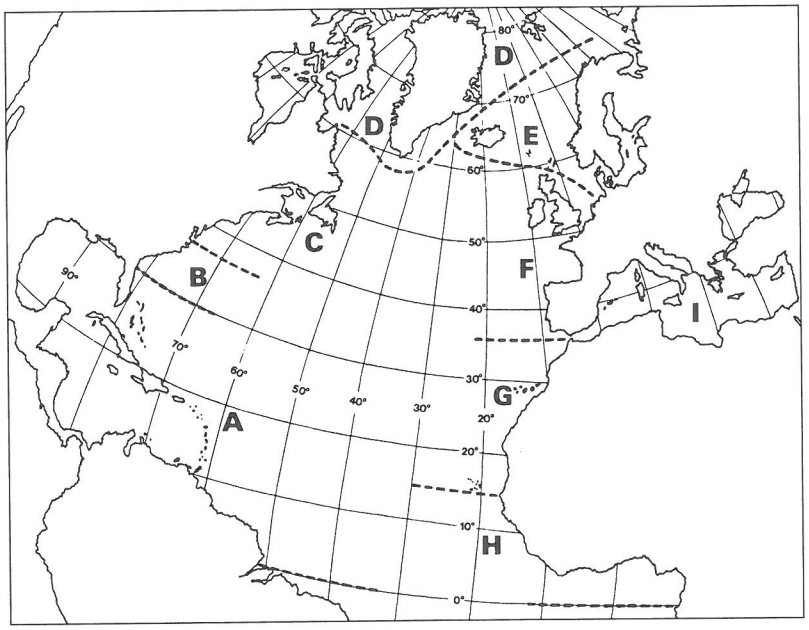
Statistical relationships between species numbers of whole seaweed floras as well as major taxonomic groups of 25 regions of the North Atlantic Ocean and the Mediterranean Sea and geographical factors as latitude, longitude, average temperatures in February and August, tidal height, and coastal length have been sought by the authors.

Compared to the seaweed distribution analyses of van den Hoek (*e.g.* 1975, 1979, 1982a, b, c, ...), focussing on rhodophyta and backed up by ecological laboratory testing, these authors used all seaweed floras and records of distribution patterns from various authors. Their analysis revealed that tidal height appeared to be inversely related to species numbers, especially of rhodophyta, whereas chlorophyta and phaeophyta species numbers were directly related to seawater temperatures in August and February.

In contrast to other biogeographic classifications, Alvarez et al. drew the boundary between the cold-temperate and the warm-temperate regions in the North Sea, with regard to a cold water related flora of Denmark, and including the whole British and Irish mainlands in the warm-temperate region. The affinity between Arctic zones proved to be somewhat low, perhaps due to restricted data taken only from Canada, southern Greenland, and Spitzbergen (Svalbard).

The authors found a segregation between western and eastern Atlantic cold- and warm-temperate floras in contrast to van den Hoek's (1975) amphiatlantic groups.
Coastal length was lacking statistical significance with species numbers.

The most surprising result was the sharp discontinuity between the eastern North Atlantic and the Mediterranean and a new distinct region of North-West Africa comprising the Canary Islands. In this sense, with regard to the OSPAR area, it is a pity that they did not include any data of the Azores and Madeira to show the biogeographic relationships between the Macaronesian archipelagos and the north-western African, Iberian and Mediterranean floras.



Symbol	Region name	Approxima latitude ext
A	Tropical Western Atlantic region	28 N-0
B	Warm temperate Western Atlantic region	37 N-28 I
C	Cold temperate Western Atlantic region	60 N-37 I
D	Arctic Atlantic region (America-Greenland)	75 -60 N
D	Arctic Atlantic region (Europe)	80 N-71 I
E	Cold temperate Eastern Atlantic region	71 N-58 I
F	Warm temperate Eastern Atlantic region	59 N-36N
G	Subtropical Eastern Atlantic region	36 N-13 I
H	Tropical Eastern Atlantic region	13 N-0
I	Mediterranean region	46 N-36 I

Fig. 72: Phytogeographic regions along the North Atlantic and the Mediterranean coasts as shown by seaweed flora affinities (from Alvarez et al. 1988).

5.1.19 MICHANEK (1979): *Phytogeographic provinces and seaweed distribution*

This classification was developed as part of an evaluation of seaweed distribution for an economic use of harvestable plant resources and production data (MICHANEK 1983).

The warm temperate region shows isotheres (summer maxima) of ~ 20-25° C, surface temperatures usually ~ 17°-25° C in summer, 10°-20° C in winter, and seasonal temperature variations of ~ 10° C. The delimitation against the cold temperate or boreal region in the NEA follows mainly VAN DEN HOEK and DONZE (1967) with a transition between warm Lusitanean and cold boreal waters at the entrance of the English Channel and between Clare Island/W-Ireland and the Faeroes. Apart from regions of upwelling water, is transparent and productivity is generally low. Eurythermic tropical species adapted to temperature changes and able to withstand lower winter temperatures are included as well as boreal species that can endure high summer temperatures. The genera *Cystoseira* and *Sargassum* partly replace *Laminaria* and *Fucus* which stretch into warm temperate waters from the boreal region. *Saccorhiza polyschides* is best developed in warm temperate waters.

The cold temperate region is characterised by a strong seasonality with winter temperatures between 0° C and +10° C, annual variations in coastal waters of 10°-20° C and great differences between top surface layers and strata below in summer. Phycologically, this is the biogeographic zone of highest developed kelp and rockweed vegetation, particularly the genera *Laminaria* and *Fucus* in the Atlantic. The cold temperate region has also assimilated eurythermic species of warm temperate origin. Some of those survive the low winter temperatures as sterile winter stands, or hibernate as spores, zygotes, or microscopic gametophytes. A delimitation against the Subarctic region is supported by the other floral discontinuity between Spitzbergen and Scandinavia mentioned by VAN DEN HOEK and DONZE (1967).

The Subarctic region shows usually but not necessarily seasonal sea ice cover. It stretches along the Murman coast to the point of regular coastal ice in winter, and, according to DUNBAR (1951, 1953) consists of mixed Arctic and Atlantic waters. Surface temperatures may rise to 5° C in the summer. The genera *Alaria, Agarum,* and certain *Laminaria* and *Fucus* species characterise this region. They are not necessarily confined to Arctic waters but make up a bigger part of the total biomass.

The delineation between the Arctic, which has almost all the year round ice cover, and the Subarctic regions was fully adopted from DUNBAR (1951, 1953).

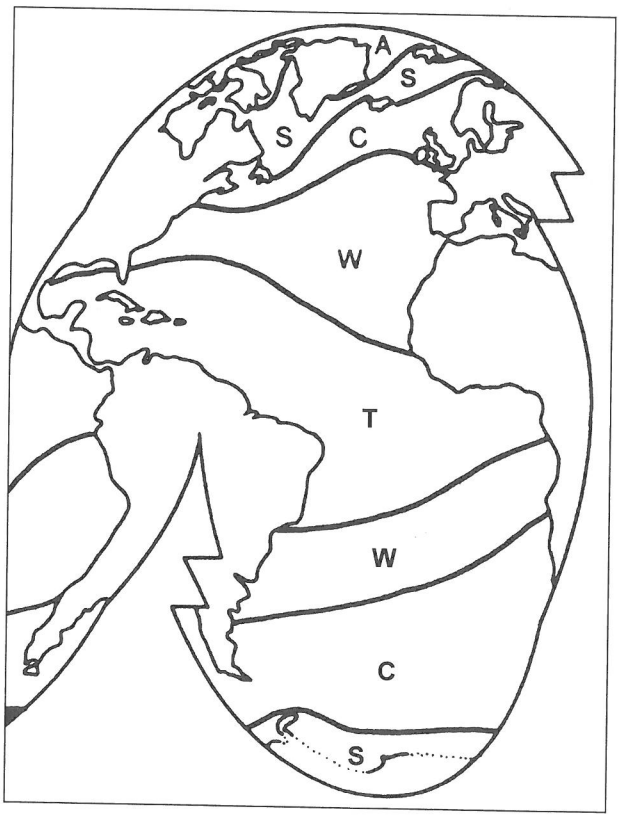


Fig. 73: Geographical distribution of marine algae. Delineation of climatic regions refer to coastal littoral and sublittoral waters (from MICHANEK 1979, clipped).
A: Arctic
S: Subarctic
C: Cold temperate
W: Warm temperate
T: Tropical

5.1.20 Hela and Laevastu (1961): *Natural regions of the oceans*

Hela and Laevastu made their biogeographical analysis in relation to near surface hydrographical factors (*e.g.* shelf areas; current regimes with related boundaries as convergences; temperature regimes) that influence distribution and abundance of species important to the fishing industry (Fig. 74). Criteria mentioned were presence and abundance of adult species, sporadic, erratic, and very rare occurrence, and abundance criterions for spawning areas. An applied branch of marine biogeography should deal with distribution and abundance of fishery resources and their population dynamics according to the authors.

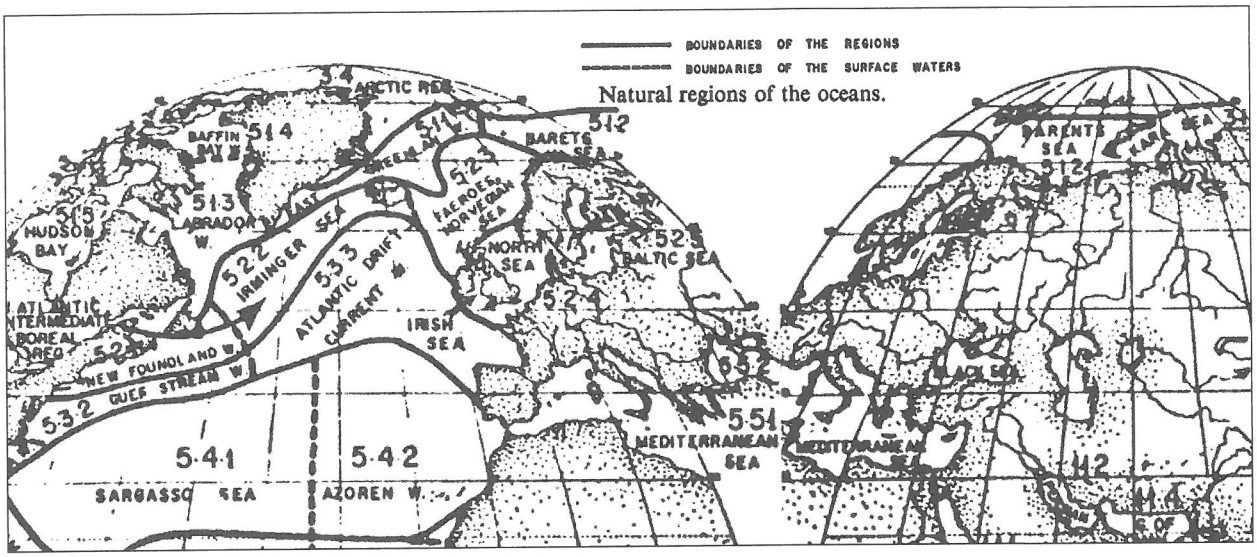
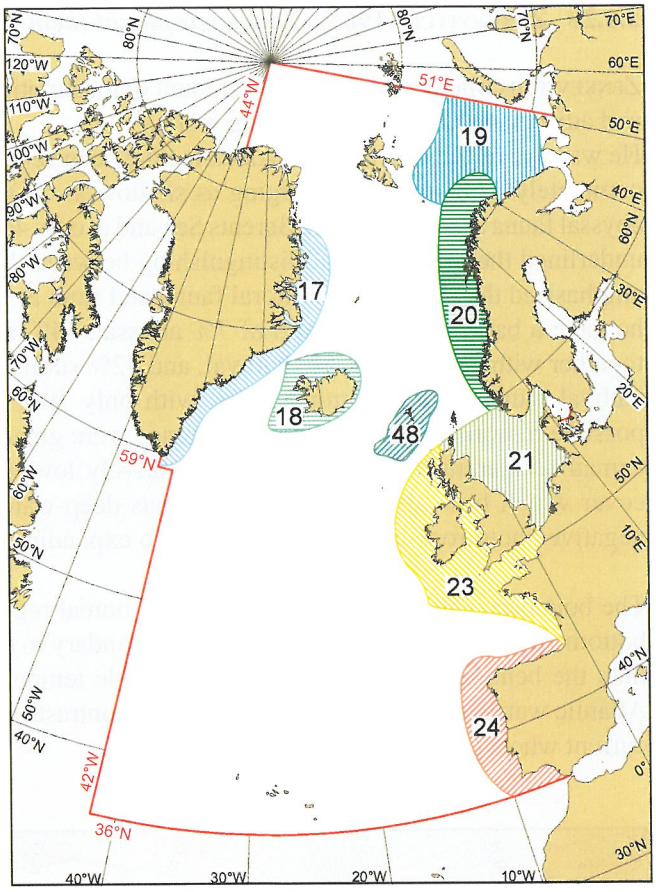


Fig. 74: Natural regions of the oceans (from Hela and Laevastu 1961; clipped).

5.1.21 Sherman and Alexander (1986): *Large Marine Ecosystems (LMEs), as global units for marine resources management*

The concept of Large Marine Ecosystems has been presented and discussed in a series of publications (*e.g.* Sherman et al. 1983; Sherman and Alexander 1986, 1989; Alexander 1992; Sherman and Laughlin 1992; Sherman et al. 1990, 1991, 1992, 1993; Sherman 1993, 1994; Sherman and Busch 1995).
This concept emerged after the 1982 UNCLOS agreement which stated that national EEZs can be established up to 200 nm from the baselines of territorial seas and granted coastal states sovereign rights to explore, manage, and conserve the natural resources in this zone. So far 49 LMEs have been identified under the lead of ICES synthesising fisheries, environmental, and productive information. Large Marine Ecosystems are relatively extensive regions, generally greater than 200,000 km^2, characterised by a distinct bathymetry, hydrography, productivity, and trophically dependent populations.
They may be within or beyond the boundaries of EEZs (Fig. 75). They might be identified and made up of submarine topography, hydrographic regimes, trophically dependent populations, commercial species, and an intersection of national claims (Sherman and Alexander 1986; Sherman 1993).
LMEs are subject to increasing stress from growing exploitation of fish and other renewable resources, coastal zone damage, river basin runoff, dumping of urban wastes, and fallout from aerosol contaminants. The LME-concept can be used to monitor living marine resources, the "health" of their habitats, and to control the structure and functioning of biological communities but the emphasis is largely on the management of marine resources, in order to sustain useable biomass yields with a strong focus on exploitable fish.
Comparative studies with LMEs could contribute to improvements in forecasting regional and global trends in marine biomass yields.

Fig. 75: LMEs of the North-East Atlantic (from SHERMAN and ALEXANDER 1986):
17: East Greenland Shelf
18: Iceland Shelf
19: Barents Sea
20: Norwegian Shelf
21: North Sea
48: Faeroe Shelf
23: Celtic-Biscay Shelf
24: Iberian Coastal



5.1.22 DUNBAR (1951/1985): *The Arctic Marine Ecosystem*

DUNBAR has published in a series of publications (1951, 1953, 1955, 1963, 1968, 1972, 1977a, 1979, 1982, 1985) a concept for the differentiation between marine Arctic and Subarctic regions. For the upper water column (200-300 m at least), marine Arctic were distinguished from Subarctic regions and open from semi-closed water bodies. In the latter region Arctic waters mix with North Atlantic and North Pacific waters and DUNBAR identified a good correlation of temperature regimes, biological production, and biogeography.

The Arctic proper was biogeographically characterised by the ecological significance of its ice cover in combination with strong seasonality and differences in productivity.

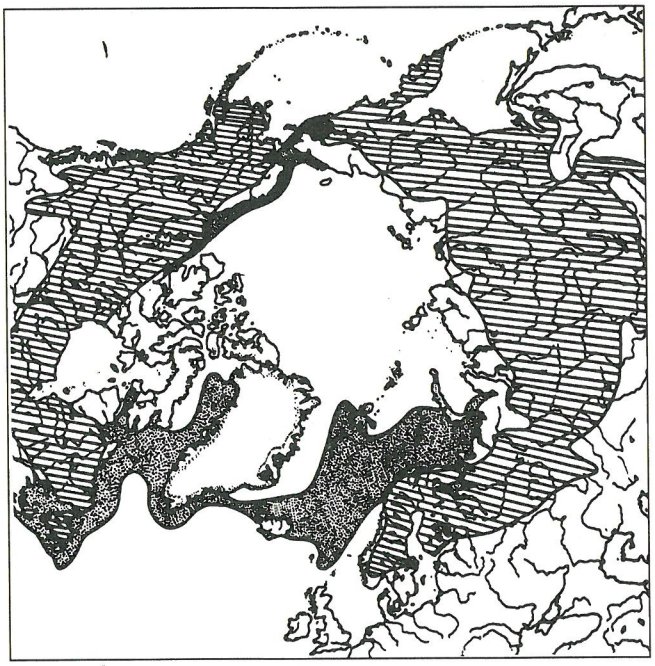


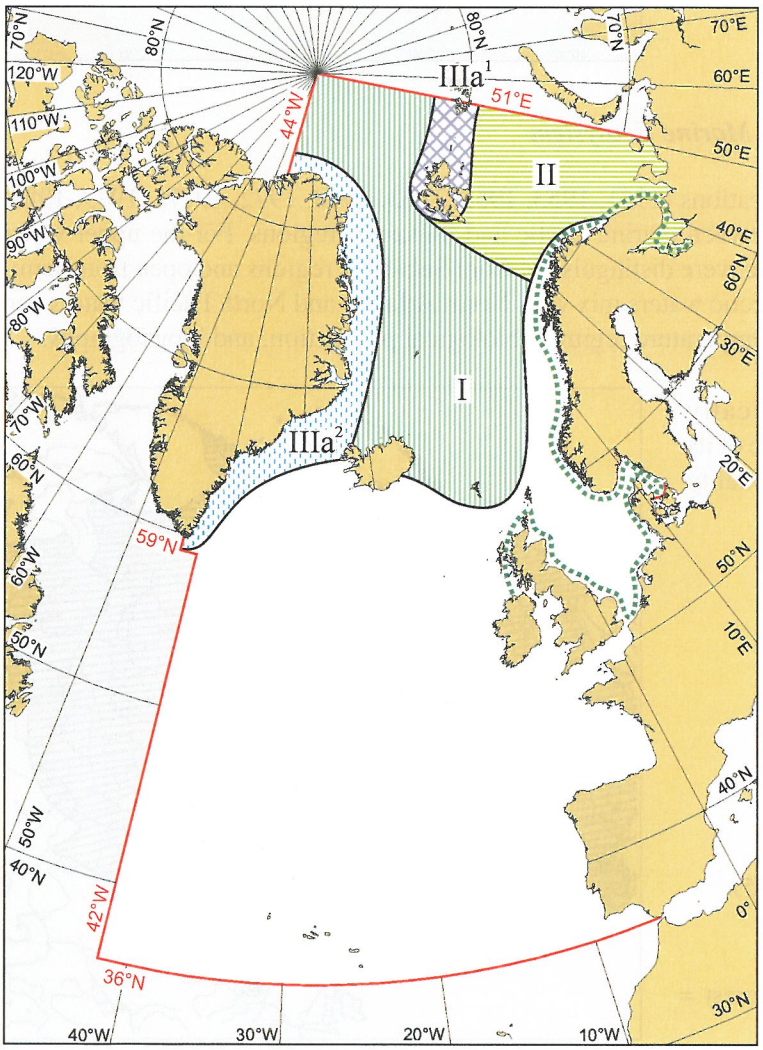
Fig. 76: Arctic ecosystems (from DUNBAR 1985).
marine Arctic = central white areas
marine Subarctic = dark-stippled

terrestrial Subarctic/high latitude forest = hatched areas

5.1.23 Zenkevitch (1963): *Zoogeographical (benthos) zonation of the Arctic*

Zenkevitch collected an enormous amount of information about marine "Biology of the Seas of the U.S.S.R." and adjacent seas in his outstanding work.
He was one of the first people to describe the occurrence of deep-sea species in shallow Arctic waters with a completely bathyal fauna emerging as shallow as 100-200 m depths in Siberian coastal waters, a pseudo-abyssal fauna at > 200 m in the Barents Sea and at only 40-50 m depth in the Nowosibirsk shallows. Zenkevitch underlined the difficulties of distinguishing between the sublittoral, bathyal, and abyssal in this region and emphasised the absence of a littoral fauna and flora as being characteristic for the high Arctic. For example he gave a bathyal benthos ratio of 7% abyssal, 14% bathyal, and 30% sublittoral Arctic endemic species together with 2% abyssal, 5% bathyal, and 42% sublittoral species of wider distribution. Hence 72% of the bathyal fauna were sublittoral forms with only 19% being true bathyal and 9% of abyssal origin. Four possible reasons for this unusual emergence were given: low surface temperatures of the high Arctic; small annual temperature fluctuations; comparatively low water transparency; and obscurity caused by the ice cover which lasts almost all the year. Thus deep-water fauna with a clear cold-water stenothermy and a negative phototropism finds no obstacles to expanding into comparatively higher levels.

The boundaries between the Arctic and the boreal regions in the North Atlantic were not the same for the bottom and the pelagic fauna. The pelagic boundary in the Barents Sea lies much farther to the north and east than the benthic boundary due to considerable temperature differences between the upper water body of Atlantic waters and the colder sea floor. This contrasts with the region influenced by the cold East Greenland current where patterns are reversed.



The western part of the White Sea was indicated as having a distinct boreal and much more seasonal and brackish character even if not marked on the map.

Zenkevitch also stressed the dissimilarity between Arctic and Pacific bottom faunas caused by the shallow Bering Strait.

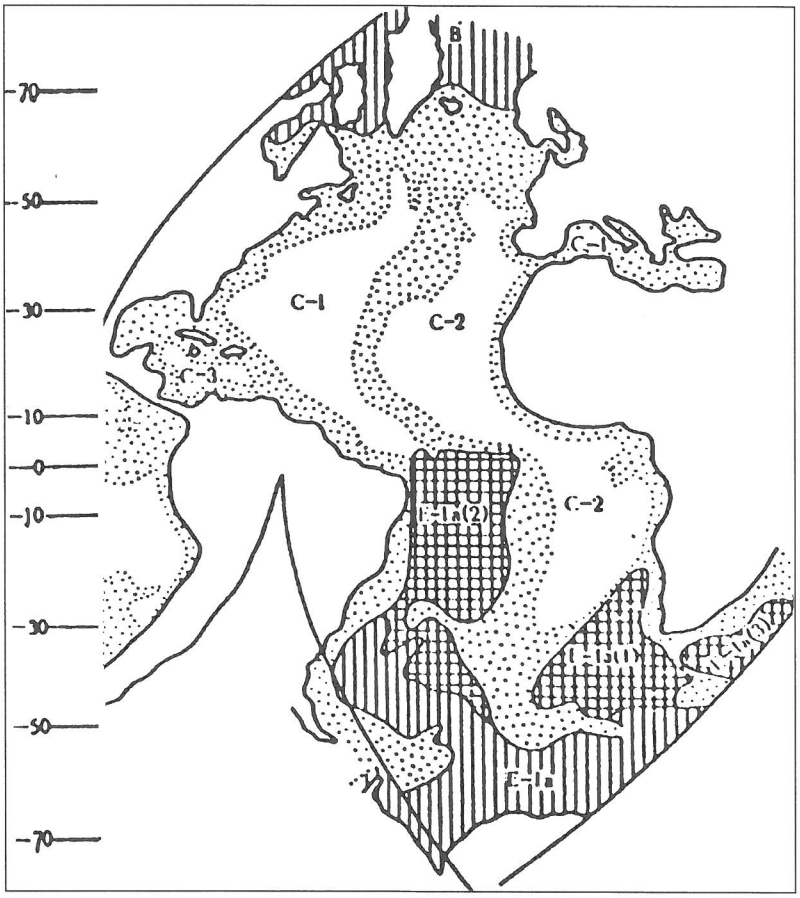
I: Abyssal Arctic subregion
II: Lower Arctic shallow subregion
IIIa¹: High Arctic shallow marine province; Siberian region
IIIa²: High Arctic shallow marine province; North American Greenland region
dotted line: propagation of the boreal littoral fauna north- and eastwards

Fig. 77: (after Zenkevitch 1963, redrawn).

5.1.24 Menzies, George, and Rowe (1973): *Abyssal Environment and Ecology of the World Oceans*

Menzies (1963) and Menzies et al. (1973) regarded the Arctic as being a separate zoogeographic region not related to the deep Atlantic. Below 2000 m there was made only a distinction between the Norwegian and the Eurasian basins in the former work. These provinces were differentiated into 5 hypothetical provinces in the later publication (legend to Fig. 78).
The Arctic divisions as well as those of the other oceans and regions (Fig. 78) were based on differences in seafloor topography, water masses, and especially temperature of depths > 4000 m, but not confirmed by faunistic material. Vertically the Arctic was subdivided into an oligohaline shallow shelf faunal zone along Murmansk and the Canadian archipelago, a nearshore shelf faunal zone, an archibenthic zone of transition, and abyssal faunal provinces as indicated in the legend below.

In a later publication (Menzies 1975) the biogeographic classification of Zenkevitch (1963, Chap. 5.1.23) was widely adopted for the Arctic region consisting of a:
High Arctic abyssal region including the deep-seas of the Arctic and the Norwegian-Greenland basins;
High Arctic shallow region between the abyss and the shore;
High Arctic brackish water subregion surrounding the Siberian, Canadian, and Alaskan shores where the fauna must adjust to seasonal changes in temperature and salinity;
Boreal littoral faunal region from Norway that represents the faunal penetration (summer) by the warm Norwegian Current;
Low Arctic shallow region between the High Arctic brackish water subregion and the High Arctic central regions. This is transitional between the Boreal Norwegian fauna and the High Arctic fauna; this time obviously referring to Arctic-Atlantic relations.



B Arctic Deep-Water Region
B-1 Norwegian province
B-2 Greenland-Fram province
B-3 Eurasian province
B-4 Siberian province
B-5 Canadian province

C Atlantic Deep-Water Region
C-1 Northwestern Atlantic province
C-2 North-Southeastern province
C-3 Caribbean-Gulf province
C-4 Mediterranean province

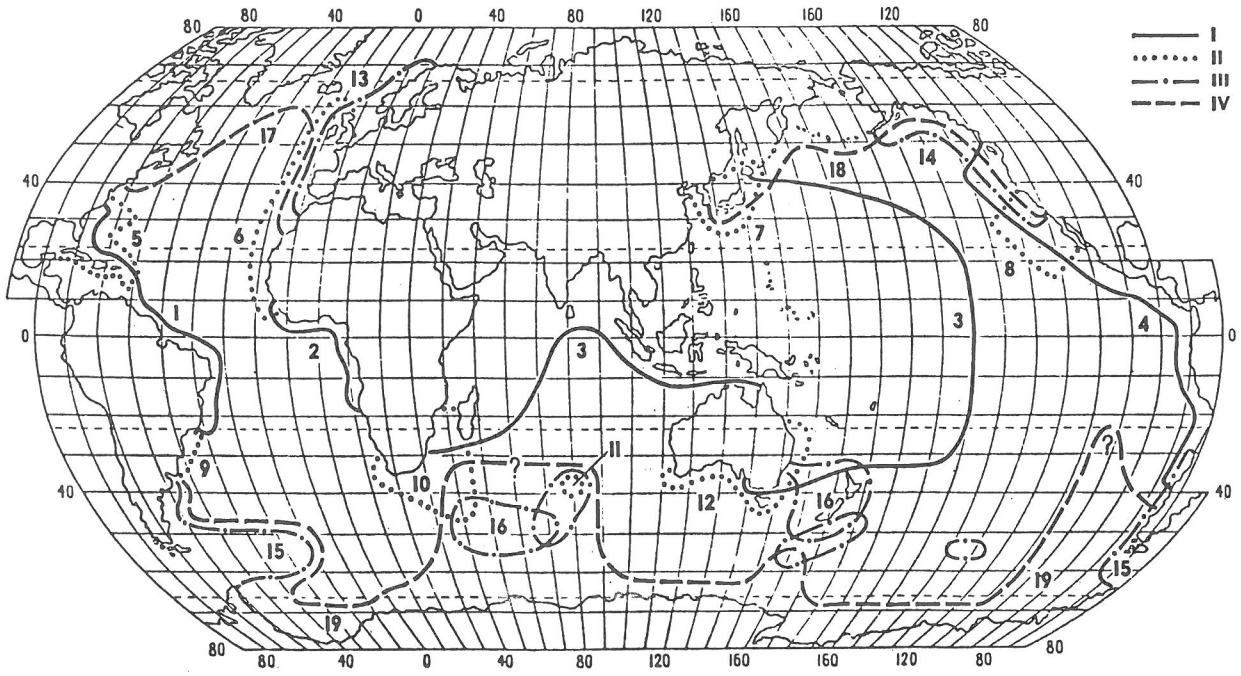
E Antarctic Deep-Water Region
E-1a Atlanto-Indian Antarctic area
E-1a(1) Eastern South Atlantic subarea
E-1a(2) Western South Atlantic subarea
E-1a(3) Southeastern Indian subarea

Fig. 78: A hypothetical scheme of lower abyssal zoogeographic regions, provinces, and areas (from Menzies et al. 1973, clipped).

5.1.25 Zezina (1997): *Biogeography of the Bathyal Zone*

This species-level biogeographic approach is based on the distribution of recent brachiopods. According to the author, it should allow the detection of the recent causes of distribution patterns and the distinction between actual and historical causes. The distribution of brachiopods that live on the outer shelf edges, and on the slopes of continents, islands, seamounts, and underwater ridges was examined at depths between 200-3000 m.
There were discriminated the following depth-related changes within the limits of the bathyal zone:
1.) The reduction of the number of latitudinal (climatic) faunistic belts from 7 global latitudinal belts at depths less than 700 m to 3 latitudinal belts of depths deeper than 700 m. Differences of physical characteristics of water masses below 2000 m are regarded as being that negligible, that hence the most important biogeographic difference lies in food supply. Food supply related to the regional productivity and depth was regarded as an important factor to the distribution of macrobenthic animals.
2.) The diminishing number of species, and
3.) The decreasing number of geographic faunistic elements with increasing depth. Correspondingly a reduction in number of faunistic provinces was identified. The simplification in the biogeographic structure of the bottom fauna down the slopes correlates with the simplification in the structure of the water masses.

Zezina stated that the productive potential of the upper slope is similar to the one on the continental shelve, that many systematic groups such as bivalves, gastropods, stalked crinoids, brachiopods, and fishes attain their maximum species number in the bathyal zone, and that regions of upwelling disturb the normal structure of bathyal benthic assemblages. The bathyal zone may have acted as a refuge and reserve for recolonisation of the shelves in periods of global climate change, which might be indicated by the occurrence of many relic species, some of which are the most primitive extant members of their groups.



Latitudinal (climatic) belts:
I, limits of tropical species distribution; II, limits for northern and southern subtropical species;
III, limits for low boreal and antiboreal species; IV, limits for the most cold-water species.

Geographic elements (indicated only the ones with relevance for the OSPAR area):
1, Caribbean; 2, West African; 4, East Pacific; 5, West Atlantic; 6, East Atlantic together with Mediterranean and Lusitano-Mauritano-Mediterranean; 13, West European; 17, North Atlantic;

Fig. 79: Geographic elements of recent brachiopods as distributed in latitudinal belts (from Zezina 1997).

5.1.26 VINOGRADOVA (1997): *Zoogeographic demarcation of the abyssal and hadal zones of the ocean*

This classification of abyssal and ultra-abyssal (hadal) zones > 3000 m depth appeared in 1956 and was published up to 1997 with only minor changes (*e.g.* VINOGRADOVA 1956, 1959, 1979, 1997).

A major conclusion was that the geographical extent of species' ranges is related to their degree of eurybathymism and that groups with a high proportion of true stenobathyal abyssal species show a high degree of endemism. In analysing relationships between adjacent regions and factors controlling distribution attention was given to fringe-like species ranges near the base of continental slopes, determined by nutritional conditions.
In the review of 2000 species of deep-sea macrobenthos she identified ~ 85% of species which were confined to only one ocean (32.5% Atlantic, 35.6% Pacific, 16.8% Indian) whereas ~ 4% were cosmopolitans. Thus she contradicted former opinions of a universal uniformly abyssal fauna.

Furthermore she recognised that the difference between faunas of different regions increases with depth.

Regional separations of the rather extensive regions had been emphasised as occurring through macrorelief features like mid-ocean ridges, elevations or continents.
Productivity of the ocean surfaces was recognised to influence the geographical distribution of the deep-sea fauna with latitudinal boundaries at ~35°-40°N but the outcome for the regionalisation of the North Atlantic was not mapped. This scheme might have been altered due to meridional deep-sea current patterns which influence the deposition of detrital snow.

The Arctic comprising the Arctic and Norwegian-Greenland basins was regarded as a subregion of an Atlantic deep-sea region but with a high degree of endemics in some faunal groups.

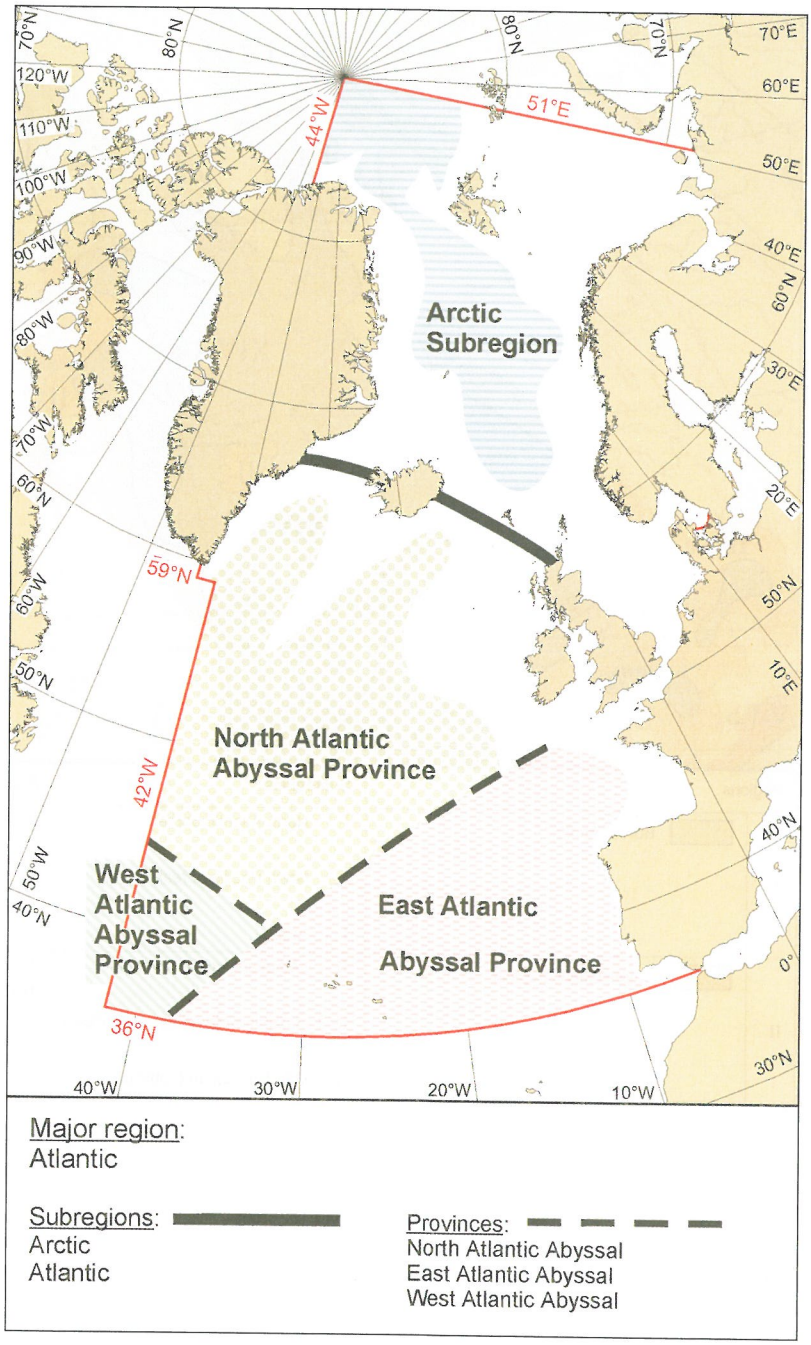
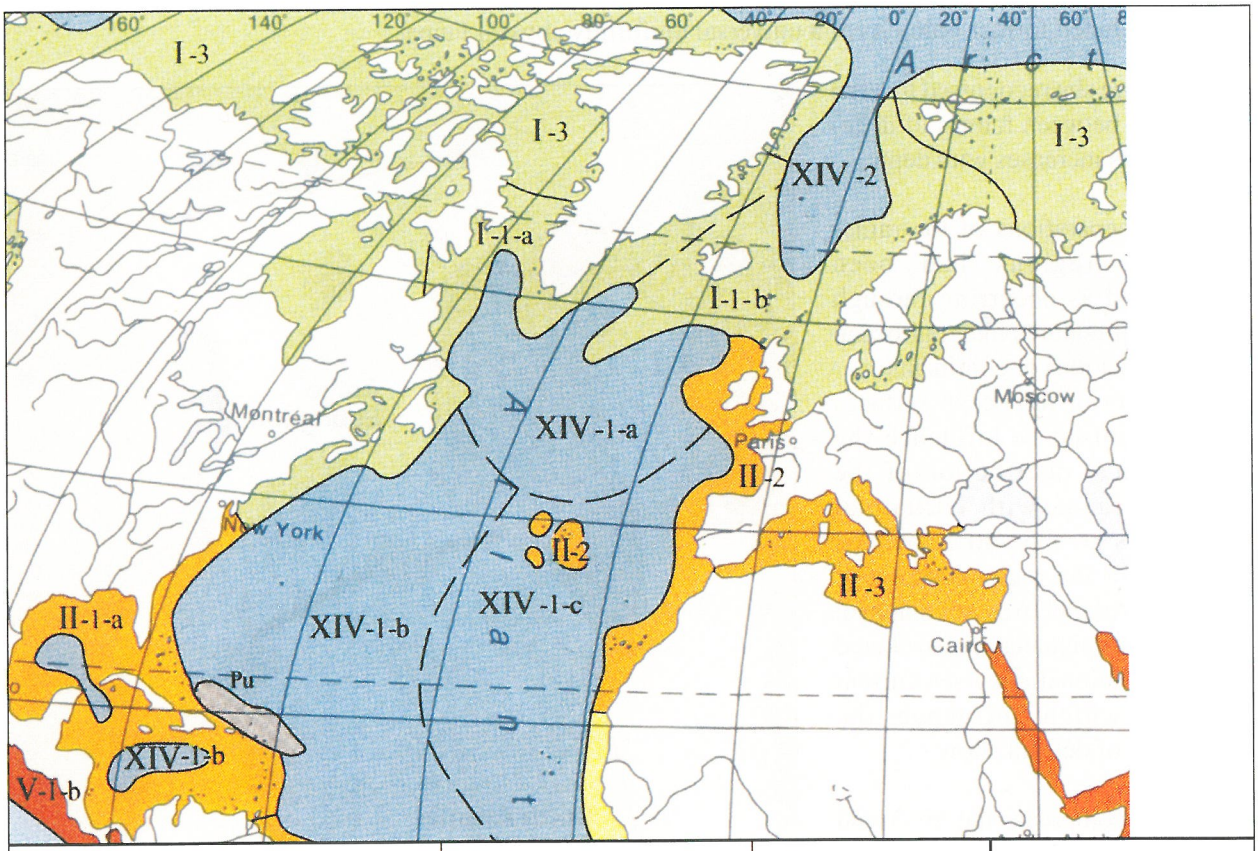


Fig. 80: Zoogeographic demarcation of the abyssal zone of the ocean (from VINOGRADOVA 1997, redrawn)

5.1.27 Vinogradova and Zezina (1998): *Zoogeographic regionalisation of the benthal in the range of continental shelf and slope, and of abyssal and ultra-abyssal zones*

This map is a synthesis of former presentations by the two authors (*e.g.* Vinogradova 1979, 1997; Zezina 1997) and is based on brachiopods of shelf, sublittoral, and continental slope zones on the one hand and various systematic animal groups of abyssal and ultra-abyssal zones on the other hand. Only one group of organisms – brachiopods – have been referred to in this map because it was necessary to apply the same uniform criteria for assessing the similarity and distinction of different faunas throughout the ocean floor. Benthic abyssal faunas were noted for their high degree of endemism with many endemic genera and even some families occurring only locally in the ocean. Major differences are between the Pacific, Antarctic, and Atlantic Oceans and a mutual relationship between the abyssal benthic fauna of the Arctic and the Atlantic was stated.



Regions		Subregions	Provinces
I	Boreal-Arctic	I -1 North Atlantic boreal	I -1-a North American I -1-b North European
		I -2 North Pacific boreal	I -2-a Asiatic-Aleutian I -1-b North American
		I -3 Arctic	
II	Amphiatlantic tropical	II -1 Atlantic-Central American	II -1-a Caribean II -1-b Brazilian
		II -2 Luzitano-Mauritanic (subtropic)	
		II -3 Mediterranean (subtropic)	
III	West African tropical		
XIV	Atlantic deep	XIV -1 Atlantic	XIV -1-a Northern Atlantic XIV -1-b Western Atlantic XIV -1-c Eastern Atlantic
		XIV -2 Arctic	

Subregion boundaries
Province boundaries
I - XV Regions
1, 2, 3 Subregions
a, b, c Provinces
Ultra-abyssal provinces

Fig. 81: Zoogeographic regionalisation of the benthal in the range of continental shelf and slope (I, II, III), and of abyssal and ultra-abyssal zones (XIV) (from Vinogradova and Zezina 1998, clipped).

6 A Biogeographic Synoptical Synthesis of the OSPAR Maritime Area (An integrated biogeographical approach of the North-East Atlantic area)

6.1 Criteria for the biogeographic classification of the OSPAR area

FORBES (1859) distinguished provinces by stating "a province is distinct so far as it is supposed to contain a certain amount of specific forms which have not been found in some other part of the same sea or ocean, but it has never any stronger support than that of negative evidence". According to WOODWARD (1856) "a province should have one-half of its species peculiar to it". Provinces established on the mixed or intermediate character of its fauna, should not be of like value with the others (FORBES 1859). But even SCHENK and KEEN (1936) who propagated the mid-point-range method (1937) proposed a subjective definition for a province (HEDGPETH 1957). Clearly razor-sharp limits can never be drawn as stated by MICHANEK (1979).

The hierarchy of HAYDEN et al. (1984) used the term "realm" for a major subdivision of the world consisting of several "regions" within which there are "provinces". The later can be justified as separable either on account of endemism or by a characteristic biotic association. Hence "biome" signifies an ecological formation in biophysiognomic terms being an ecological conceptualisation in contrast to "realm" that describes a geographic division.

According to BRIGGS (1995) two fundamental divisions of the marine biome are those between the benthic realm and the pelagic realm, and each of these may be subdivided into a number of depth zones (Fig. 12) as well as into a series of horizontal regions, provinces, and subprovinces. The continental shelves are considered to be part of the benthic realm including the neritic water column. The eastern Atlantic has been identified as belonging to the hierarchical level of a region by BRIGGS (1995).

Provinces are subjective appraisals of biogeographic specialists dividing traditionally major temperature realms into provinces according to HEDGPETH (1957). For other authors provinces describe an index of 50 % endemism (WOODWARD 1856), or marine temperature regimes according to VAUGHAN (1940), STEPHENSON (1947), or to some extent to DUNBAR's view (1979) (Fig. 43). Statistical analyses and divisions after the ranges from mid-points of all species can distinguish provinces (SCHENK and KEEN 1937; EKMAN 1953) but latter method does not take into account presence of different species due to different habitats and special features out of the "normal range", *e.g.* cold-water species within regions of upwelling in a warmer surrounding, and has been regarded as impractical on this level (HEDGPETH 1957).

Within a biogeographic province there should be subareas, each of which supporting its own endemic biota, as stressed by VERMEIJ (1996). Counting and reporting species of a given biogeographic province on a larger scale (*e.g.* boreal region/BRIGGS 1974; cool-temperate zone/VAN DER SPOEL and HEYMAN 1983) might therefore be misleading in characterising the whole province. Documentation of species-level patterns in space and time has to reflect the appropriate geographical (and time) scale.

LLORIS et al. (1991) discussed the ranking of biogeographical units in a hierarchy with regard to the Macaronesian region and stressed the insufficiency of such a system in a dynamic situation on the temporal scale.

One of the central ideas of biogeography is that geographical subdivisions associated with a specific physio-oceanographic regime support a characteristic account of endemic organisms or related biocoenoses.
Thus the most logical procedure in marine biogeography is to look for natural floristic and faunistic boundaries (frontiers) and to compare them with areas of changing environmental factors to seek a causative relationship. If one defines types of ranges in order to combine different species with similar geographical ranges into groups there is no reference to the systematic position of the species or their genetic and cladistic relationships. The species-level approach allows detection of the recent causes of distribution patterns and enables a distinction between actual and historical causes. All taxa higher than species can show historical relationships between faunas but do not necessarily reflect the strength of contemporary biogeographical barriers. For instance there are no planktonic and few benthic endemics between the Middle and the North Atlantic above species

level. The conclusion is that there is a recent biogeographical boundary but with not enough time as needed for the development of endemics in higher taxa (ZEZINA 1997).

As mentioned in chapter 5 there is no approved methodology for marine biogeography and also in this case the methods used follow a certain purpose (getting practical and useful units for a representative system of MPAs). EKMAN (1953) and VAN DEN HOEK and DONZE (1967) did not find any effective barrier to distribution along the European coasts but more a Boreal province which is bounded by intermediate zones with representations from both neighbouring faunas. Facing this situation and the circumstance that endemism rates obviously differ considerably between different species groups and their taxonomic levels, other criteria for a biogeographic description of the OSPAR area had to be developed. Starting with a given region (OSPAR area) that had to be classified, endemism rates of certain taxa could not be used to classify the whole three-dimensioned space with its very different ecological conditions because of quite contradictory results in different taxonomic groups at different regions or bathymetric zones. It was therefore clear that different criteria needed to be used for this region-based biogeographical classification.

Another relevant fact is that the Atlantic, being the youngest ocean (Chap. 3.1), has had the least time to develop a broad selection of endemic species. This is even more valid for the North Atlantic and the Arctic due to major fluctuations in climate regimes (Chap. 3.4; Fig. 32) since the late Tertiary. Among biogeographers there has been a lot of debate about the question how long speciation needs to take place and the means by which it is forced (*e.g.* BRIGGS 1995).

Conspicuous and coherent geographical entities vertically delimited by the outer shelf-break (Chap. 6.2.) have been characterised by described biogeographic patterns but mainly in relation to water mass characteristics. Above the 1000 m isobath there were defined three pelagic provinces (Cold Arctic Waters, Cool-temperate Waters, Warm-temperate Waters) (Chap. 6.3.1; Fig. 104) which function as higher units for the hierarchical differentiation of shelf, upper continental slope, neritopelagial, and ice-cover influenced areas (Chap. 6.3.2; Figs. 104, 105).

In Arctic regions the role of ice related biocoenoses and ice-edge phytoplankton blooms as a base for arctic food webs is evident (Chaps. 3.5; 3.5.1). On the other hand the ice cover is limiting ordinary marine biotic patterns by reduction of incoming radiation (Chap. 3.4) and thus suppression of algal growth. High phytoplankton concentrations and an enhanced pelagic productivity are restricted to marginal ice zones and polynyas. Therefore character and duration of ice cover *i.a.* acting as a substrate for biota and in addition fresh water influence (Chap. 3.3) combined with water depths/shelf-influence (benthic-pelagic coupling, see chapters 3.5; 3.5.1) serve as criteria for a differentiation and classification of Arctic provinces.

The designated "biological shelf" areas, unlike the geographical/topographical shelf of < 200 m depths, build one unit together with the overlying neritopelagial waters (VAN DER SPOEL and HEYMAN 1983; BRIGGS 1995) and the ice cover (inverted benthal) in Arctic areas. Above that they are characterised by current patterns and water masses of a specific temperature regime and physio-oceanographical features as *e.g.* upwelling areas, banks and seamounts, ice-edges, and polynyas which shape biological distribution patterns.

However within shelf, neritic, and ice-cover influenced provinces covered by the OSPAR area and presented in the classification of this study, there are partly such high biotic similarities between subordinate provinces within one superordinate pelagic province characterised by water masses (Cold Arctic, Cool-temperate, Warm-temperate) (Chap. 6.4), that there can be rarely given a differentiation criterion with an endemism rate being valid for the entire area and its organisms. Therefore a province of this study describes more a geographic division with physiographic peculiarities that support certain species assemblages and biocoenoses and the hierarchical relationship in the context of the entire Atlantic-Arctic Ocean system.
It is important to bear in mind that delimitations marked on the biogeographic maps (Figs. 104-107) are rarely sharp biological distribution limits but in most cases gradual transition zones like a sequence of species arrayed along a gradient and with only more or less distinct discontinuities in the geographical replacement of species within the biotic assemblages.

The biogeographic patterns found (Chaps. 5.1 ff.; 6.2; 6.3.1-6.3.3) have been put into order producing a scheme of the hierarchical biotic relationships and reflecting the fitting into the context of the entire Atlantic-Arctic Ocean realm system (Chap. 6.4) and furthermore transferred into maps (Figs. 104-107).

In this study the terminology of HAYDEN et al. (1984) as cited above has been used for describing different aspects of biogeography with biomes as an conceptualisation of ecological formations in biophysiognomic terms. The hierarchical line realms – region – subregion – province – subprovince, describe geographic hierarchical subdivisions.
In this study the term province describes a geographical unit with either a higher rate of or peculiar endemism, or more often an oceanographic constellation that supports a characteristic biotic association.
The term zone is used in this study for a vertical delineation between different bathymetrical strata (Chap. 6.2).

Where existing, the traditional systematic nomenclature has been used to name the different biogeographic provinces (abandoning the Celtic province of FORBES 1859). However the term "Lusitanean" which is commonly used synonymously to "warm-temperate", derived from the Latin Portuguese name, does often not seem to be adequate to describe species with a distribution range up to northern Scotland or even beyond.

6.2 The vertical zonation

Vertical zonation and delimitation of distribution patterns is even more complicated than in the horizontal dimension.

As STEELE (1975) pointed out "there is no reason to expect the biogeographic regions to have the same distribution at the surface as in the deeper waters. The distribution of each should be considered separately and cannot be represented by a single line on a map". "Beyond the limits of shelves, with increase in depths and decrease of differences in the temperature-salinity characteristics in different climate zones, the borders of biogeographic subdivisions tend to expand" as considered by GOLIKOV et al. (1990), being valid for the pelagos as well as for the benthos. Generally speaking the geographical extent of species' ranges is related to their degree of eurybathy and increases with increasing depth or, in other words, the greater the amplitude of vertical distribution of a species the wider its range (VINOGRADOVA 1997).

Availability of light is a characterising factor in the vertical dimension especially for phytal life being in addition highly dependent on epipelagial surface temperatures (MICHANEK 1979; VAN DEN HOEK 1982a, b; LÜNING 1985; ALVAREZ et al. 1988; VAN DEN HOEK et al. 1990). In addition to temperature, being the most decisive factor, changes in light conditions, hydrostatic pressure and pycnoclines, changes in sediment structure and availability of nutrients, isotherms and thermoclines, different currents in different water masses in different depths, perpendicular turbidity currents on slopes, disturbances in environment conditions, and a lot of additional factors form complex patterns of vertical zonation being different in different latitudes due to different water masses and the phenomenon of emergence and submergence (Chap. 3.2).

Below the euphotic zone, deep-sea communities are entirely dependent on the rain of detrital material and some rare larger carcasses from the pelagic realm and to lesser extent on downslope transport of matter (Chap. 3.2). The only exception to this is in the extraordinary hydrothermal vent communities around the oceanic ridges, which are essentially independent of resources from the overlying water column and are self-reliant on a chemosynthetic sulphur economy (JANNASCH and MOTTL 1985; GRASSLE 1985, 1986; PARSON et al. 1995; VAN DOVER 1995; SALDANHA et al. 1996; DESBRUYÈRES and SEGONZAC 1997; GEBRUK et al. 1997; TUNNICLIFFE ET AL. 1998).

In an early treatise (VINOGRADOVA 1962) about the "vertical zonation in the distribution of deep-sea benthic fauna in the ocean" VINOGRADOVA identified a maximum species number of sponges, holothurians, and decapods at depths of ~2500-3000 m. This correlates with PINEDA and CASWELL (1998) who stressed the parabolic curve shape of macrobenthic diversity with maxima of gastropods and polychaetes at about 3000 m depths

as being typical bathymetric patterns on slopes, but which was already emphasised by Rex (1981, 1983). In the Arctic a maximum diversity in isopod species has been described as lying between 320 and 1100 m (SVAVARSSON 1997; SVAVARSSON et al. 1990), or 750-1000 m (SVAVARSSON et al. 1993), respectively ~800 m (SVAVARSSON 1987). No depth related diversity patterns could be found in Arctic waters for amphipods by BRANDT (1995), BRANDT et al. (1996), and WEISSHAPPEL and SVAVARSSON (1998).
Ribbon-like arrays of species distribution changing with depth on the NWA continental slope were described by ROWE and MENZIES (1969) being influenced by sediment change and currents. REX (1977) showed that faunal similarity decreases very rapidly below ~1000 m with faunal replacement being much more rapid in the epifauna than in the infauna on the NWA slope. GARDINER and HAEDRICH (1978) analysed upslope and downslope distribution boundaries of echinoderms, crustaceans, fish, and molluscs and recognised a zone of dense boundary concentration between 1200 and 1600 m.

HAEDRICH and MERRET (1990) concluded that they could find little evidence for faunal zonation or communities from their examinations of demersal fish in the North Atlantic but the same authors published an atlas of demersal fishes in the North Atlantic with distinct vertical zonations (HAEDRICH and MERRET 1988), and developed a scheme of individual bathymetric ranges in the Porcupine Seabight with a distinct discontinuity at ~ 1500 m on the base of their analyses (Fig. 83). This emphasised a pronounced and common basic change in the near bottom fish fauna at around 2000 m at the slope/rise transition (MERRET and HAEDRICH 1997). VINOGRADOV (1968) described markedly vertical discontinuities in pelagic taxonomic composition at ~1000 m and ~3000 m in Subarctic waters and presented a scheme of the vertical zonal subdivision of the pelagic fauna (Fig. 82).
An even more detailed scheme of vertical subdivisions related to latitudinal differences was presented by VAN DER SPOEL and HEYMAN (1983). ANGEL (1991, 1993) showed a constant maximum species richness of planktonic ostracods at 1000 m depth along the 20°W meridian between ~3°N and ~45°N. There is a clear break in vertical species ranges for chaetognaths at 500 m in the NEA according to PIERROT-BULTS (1997). CARNEY et al. (1983) stressed that light intensity and temperature have been looked at but biological interactions as predation and competition had received almost no attention for explanation of vertical pelagic patterns. FASHAM and FOXTON (1979) emphasised the 1000 m isobath being a vertical delimitation between layers above that are affected by diurnal migration effects and layers below that differed little between day and night. MERRET (1986) further segregated meso- and bathypelagic ichtyofauna on the continental slope into obligatory or facultative pseudooceanic species.

BRIGGS (1995) noted that macroinvertebrate distributions general tend to show major changes in species composition between 400-600 m, about 1000 m, and between 1400-1600 m. GAGE and TYLER (1991) indicated exactly the same discontinuities for benthic zonations. They also showed the marked change at 1000 m depth and suggested a further break at ~2000 m for four main echinoderm groups in the Rockall Trough (Fig. 89). LE DANOIS (1948) has previously recognised a markedly change in species composition below 1000 m and set the influence of the continental margin on fauna at a vertical delimitation of 1000 m. A very drastic change in macrofaunal composition between the upper continental slope which had close similarities with the shelf and the lower continental slope and rise of the NWA was presented by ROWE et al. (1982) (Fig. 85). Also the analysis of HECKER (1990) showed a clear discontinuity between the upper and middle continental slope off New England (Fig. 86). GRASSLE et al. (1979) classified the vertical distribution of different macroinvertebrates in the NWA (Fig. 87). Their clusters showed marked discontinuities between 530 m and 1102 m for gastropods, 478 m and 1102 m for ophiuroids, whereas the cluster discontinuity was deeper for polychaetes between 1400 m and 1750 m as well as for cumaceans with a gap between 1102 m and 1470 m. Similar vertical distribution patterns were found by SIBUET (1977, 1979) for echinoderms. SOUTHWARD (1979) described a distinct discontinuity for pogonophores at ≥ 1000 m between more locally distributed upper slope species above and species below which tend to show more widespread horizontal distributions.

Because the greatest vertical changes in temperature, salinity, and O_2 concentration all occur within the top 1000 m there would be no great changes in environments influencing zonation below according to CARNEY et al. (1983). These authors assume a distinct shelf fauna above 1000 m, a distinct abyssal fauna below 2000 m, and an indistinct slope fauna recruiting immigrants from both zones above and below. Zezina and VINOGRADOVA

(1998) combined shelf, sublittoral, and continental slope on the one hand and abyssal with ultra-abyssal on the other hand for their classification and used a delimitation between their benthic units that seem to follow roughly an isobath between 700-2000 m.

This vertical boundary of 1000 m was used also for the high latitude and Arctic units despite the phenomenon of polar emergence. AAGAARD et al. (1985) described a pronounced Atlantic water influence down to depths of nearly 1000 m in the northern seas. SVAVARSSON (1997) accentuated a depth of 1000 m being a vertical boundary below which the diversity of isopods differs considerably between North Atlantic and Arctic waters on either side of the Greenland-Iceland-Faeroe Rise. SVAVARSSON et al. (1990) found a significant zonation on the upper continental slope from an analysis of the Greenland-Norwegian Sea with a discontinuity of eight shallow boundaries and twelve deep boundaries between 800 and 1200 m depth with depths > 1000 m being a major distinction for their sampling stations related to species composition (Fig. 90). VINOGRADOVA (1997) argued that the Arctic deep-sea fauna might have been formed by repeated descents of the shelf fauna under the influence of temperature and salinity oscillations and regarded the Arctic basin being populated by a pseudo-abyssal fauna. On the other hand she also used an isobath somewhere at ~ 2500 m depth in her zoogeographical map to delimit the Arctic deep-sea basins from shallow seas.
The geographical as well as the vertical distribution of polychaetes usually deviates from that of other taxonomic groups (FAUVEL 1959; HOLTHE 1978; GRASSLE and MACIOLEK 1992) as being also visible in figure 87. It was shown for terebellomorpha polychaetes with a distribution centre in the deep Norwegian-Greenland basin that "Arctic" elements colonise the benthal of adjacent areas in decreasing diversity with decreasing depth (HOLTHE 1978).

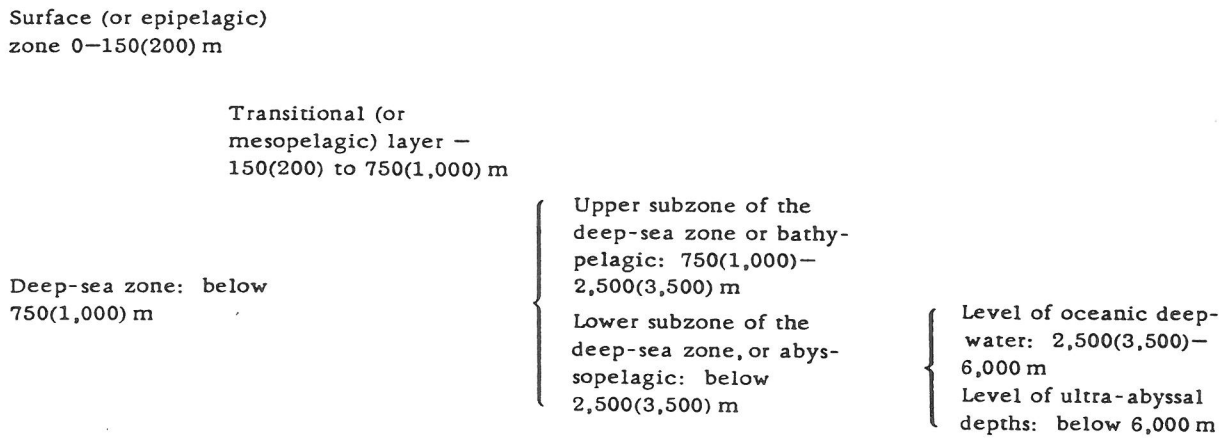


Fig. 82: Scheme of the vertical zonality of the pelagic fauna (from VINOGRADOV 1968).

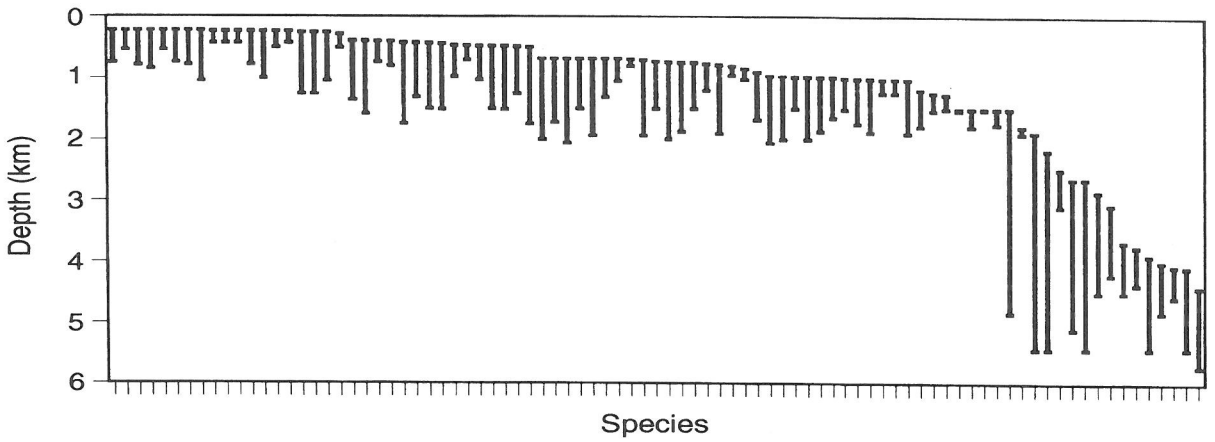


Fig. 83: Individual bathymetric ranges of deep demersal fish species on the slope and rise of the Porcupine Seabight and Abyssal plain (from MERRETT and HAEDRICH 1997).

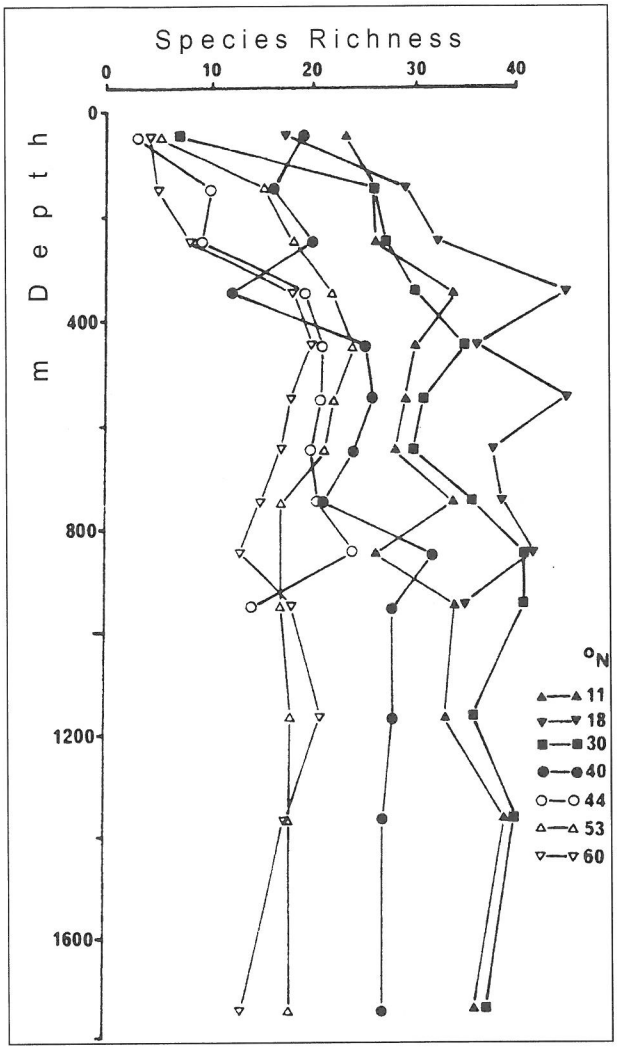


Fig. 84, left: Profile of the numbers of planktonic ostracods at each sampling horizon routinely sampled at approximately 10° intervals of latitude approximately along 20°W, showing that maximum richness is consistently at about 1000 m, despite the reduction in species richness at latitudes higher than 40°N (from ANGEL 1991, 1993).

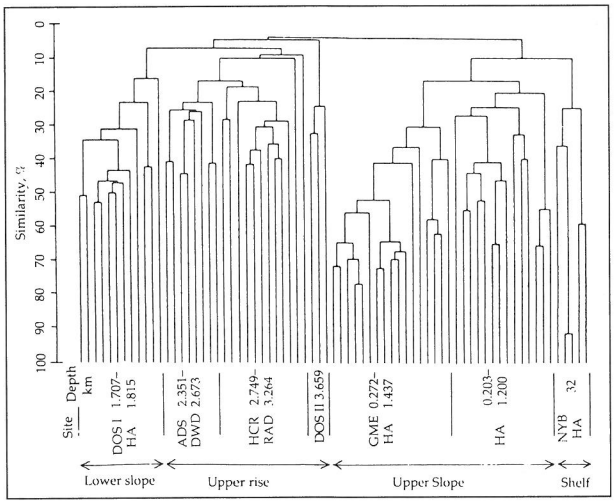


Fig. 85: Classification of macrofauna in Birge-Ekman box-cores from various sites along the U.S. NW-Atlantic continental slope and rise (from Rowe et al. 1982).

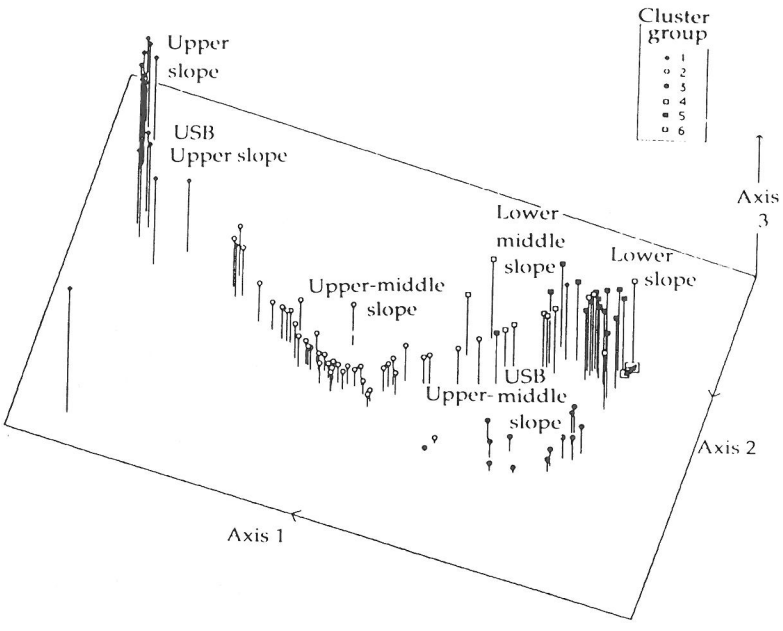


Fig. 86: Ordination by means of detrended correspondence analysis of megafauna off New England (from HECKER 1990).

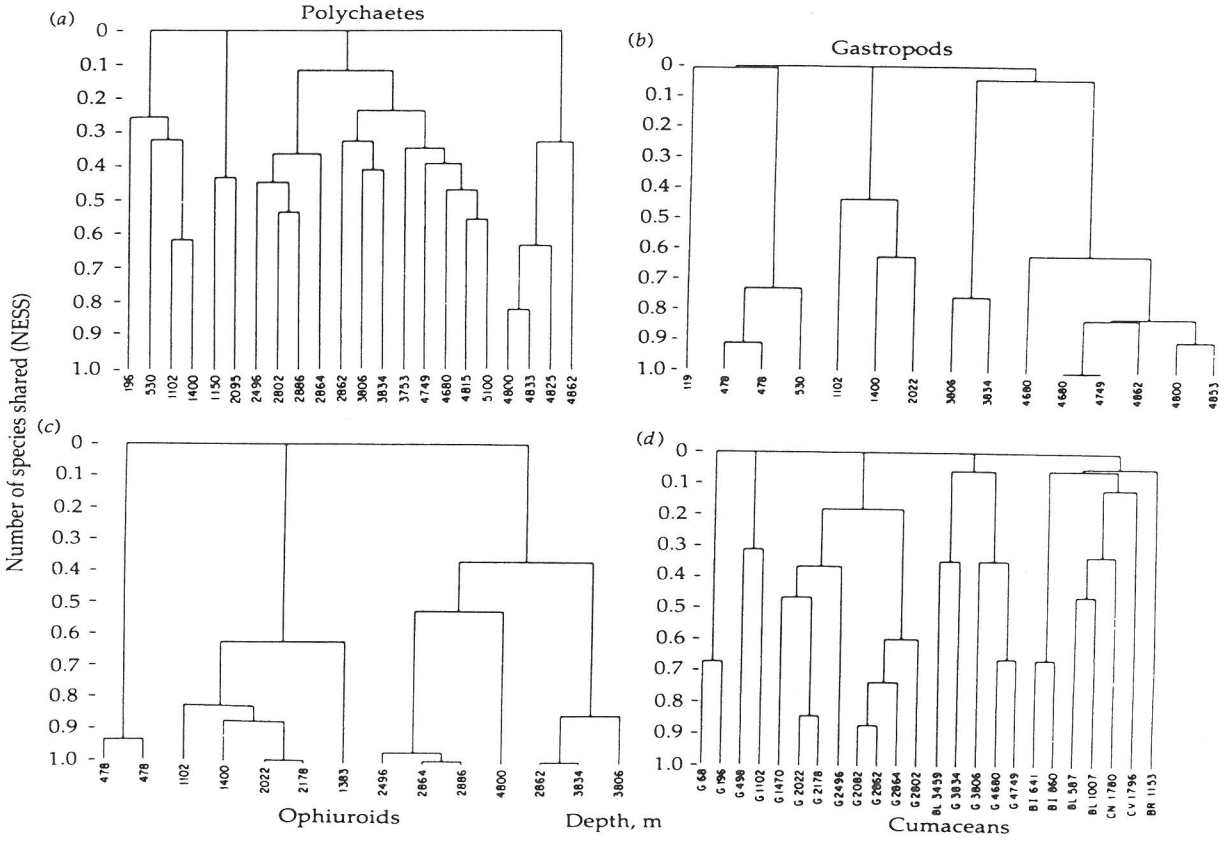


Fig. 87: Classification by NESS similarity of different macrofaunal taxa in epibenthic sled hauls from the Gay Head-Bermuda transect (x-ordinate is depth in m) (from GRASSLE et al. 1979).

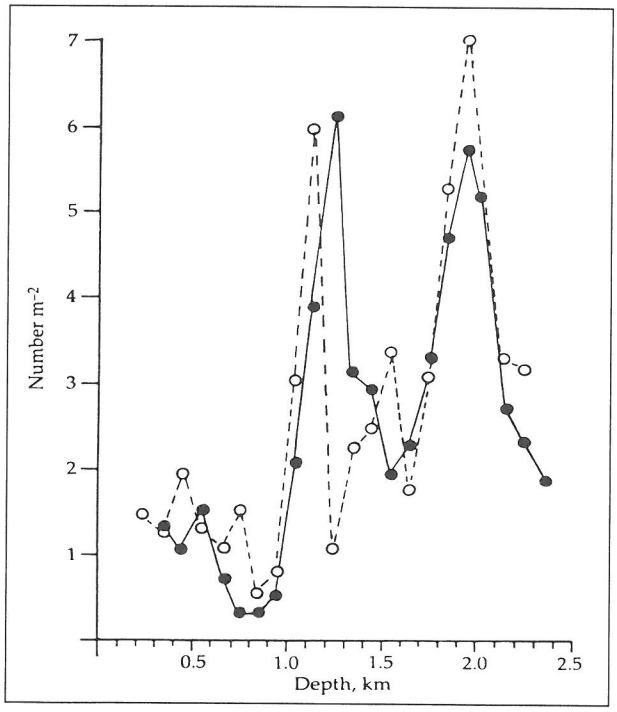


Fig. 88: Depth distributions of total megafauna from two photo-sled surveys off New England, NW-Atlantic; open circles: Nov. 1984; closed circles: May 1985 (from MACIOLEK et al. 1987b).

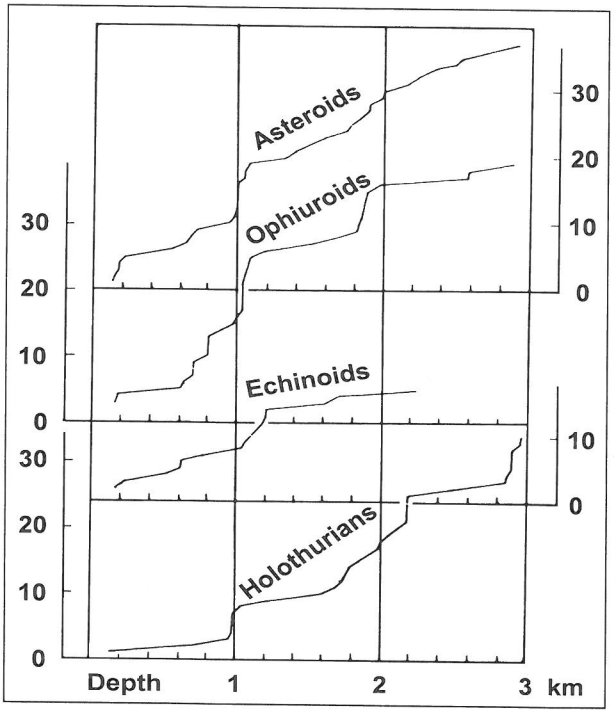


Fig. 89: Cumulative addition of species of the four main echinoderm groups in trawlings at different depths along the depth gradient in the Rockall Trough, NE-Atlantic (from GAGE 1986).

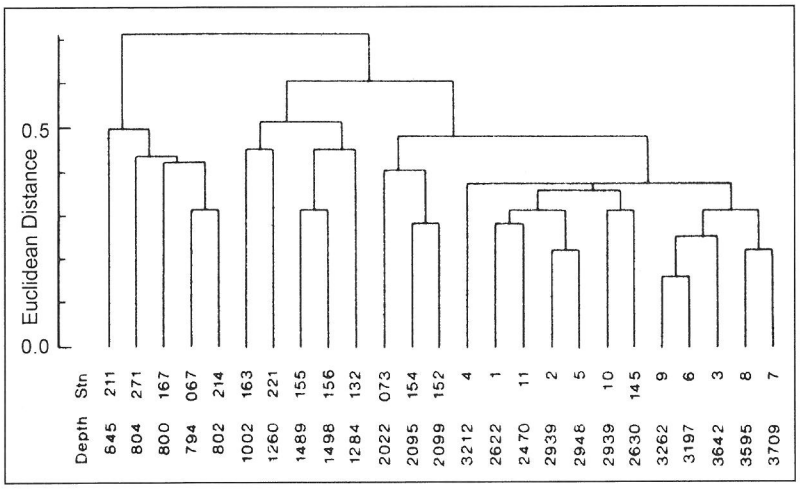


Fig. 90: Vertical classification of sampling stations after species composition in the Norwegian-Greenland Seas within a bathymetric range from 845-3709 m (from SVAVARSSON et al. 1990).

THIEL et al. (1996) compared adaptations of species to cold environments of polar and deep seas. In general deep-sea organisms encounter higher temperatures and considerably higher pressures to which they have to adapt in morphology and physiology. Availability of nutrients is another important factor that differs significantly in both environments with consequences for foraging behaviour and metabolism. However many deep-sea species have been found emerging to very shallow Arctic waters and, *vice versa*, some shallow water low Arctic species descending into deep Arctic waters. MADSEN (1961) delimited the depth of faunal change composition in the Arctic with 12-360 m, GOLIKOV et al. (1990) described the boundary between Arctic "deep-sea" and shallow Atlantic boreal biogeographic units in the White Sea, Norwegian fjords, and eastern parts of the Barents Sea being at 40-30 m depth, or sometimes even shallower, whereas Menzies et al. (1973) indicated even depths < 10 m. HESSLER et al. (1979) and KUSSAKIN (1973) described the emergence of deep-sea isopods in shallow waters of the Arctic, as well as of Norwegian and West-Swedish fjords. Dahl (1979) mentioned the presence of deep-sea gammarids at 800 m or 400 m respectively off Norway. ZENKEVITCH (1963) introduced the term "pseudo-abyssal" for shallow waters in the Arctic (*e.g.* 150 m in the White Sea, 200 m in the Barents Sea) showing fauna of a dominant bathyal character. BOUCHET and WARÉN (1979) suggested an upper limit of 1200 m for Arctic abyssal fauna besides records of abyssal molluscs at 20 m depth at NE-Greenland and set out the occurrence of bathyal fauna all along the continental slopes of NE-Greenland, Spitzbergen, Siberia, and Norway reaching up into shallow waters. In addition they described the distribution of this emerged bathyal fauna extending amphiatlantic submerged southward as far as the Bay of Biscay and the northern USA.

Menzies et al. (1973) emphasised an "Archibenthal Zone of Transition" (AZT), beyond which are deep sea species and which could be arrayed again in different bathymetric strata. Following this idea might justify a concept of a biological shelf boundary instead of using the topographical/geographical shelf boundary (200 m isobath) for a vertical zonation. This concept is dividing species of eurybathic and/or eurygraphic and/or eurythermic ecological behaviour which live in archibenthal depths from "pure" deep-sea species. In addition there is the phenomenon of polar emergence and tropical submergence of marine species which is related mainly to the thermal potencies of marine species, which applies to a lot of species of both, benthos and pelagos, and which makes vertical differentiation on a global (OSPAR) scale even more difficult (LE DANOIS 1948; ZENKEVITCH 1948/1949; EKMAN 1935, 1953; HEDGPETH 1957b; DE LATTIN 1967; VINOGRADOV 1968; GLÉMAREC 1973; MENZIES ET AL. 1973; VAN DER SPOEL AND HEYMAN 1983; VINOGRADOVA 1997; ZEZINA 1997).

As mentioned in chapter 3.1 there might be hypoxic conditions below highly productive surface waters in regions of upwelling. Vertical zonation as well as horizontal distribution patterns can differ considerably in those regions (MERRET and HAEDRICH 1997).
The approach of this study is based on an appreciation, that the boundary between the "biological shelf" (including the archibenthal) and the deep sea biome shifts from roughly ≤ 2000m depth in the south of the OSPAR area (36° N latitude) to less than 100 m depth in the high Arctic. However, to get practical and useful units as described in chapter 1 the biogeographic maps show a vertical subdivision at the 1000 m isobath

instead of several ribbon-like fringing isobathymetric layers along the continental slopes for a vertical zonation of the benthos which would somehow have to be combined with bathymetric strata of the pelagos.
This approach has been taken in the knowledge that the appropriate delimitation for a higher statistical percentage of deep sea species is suggested to be at greater depths in the south and more shallow in the Arctic.

Thus, figure 91 shows the first main biogeographic segregation between oceanic holopelagic and deep-sea areas and neritic shelf and upper continental slope areas using the 1000 m isobath for delimitation. The 1000 m delimitation of biogeographical units between shallow and deep seas in the Arctic and the Norwegian-Greenland basins follow the outer continental margin, which is deeper in the Arctic than at many European continental shelf breaks at mid-latitudes. Concluding it should be stressed that this vertical delimitation should not be regarded as depicting an upper limit for Arctic deep-sea species due to the well known fact that deep-sea species might virtually "crawl up the beaches" in the Arctic and due to the aim of this study to designate a practical number of biogeographic units in spite of three-dimensioned patches multiple strata/layers. Rather it depicts more a lower limit of some Arctic shallow water (sublittoral) species (ZENKEVICH 1963) despite the polar submergence of some shallow cold water species into deeper Arctic waters (MENZIES et al. 1973).

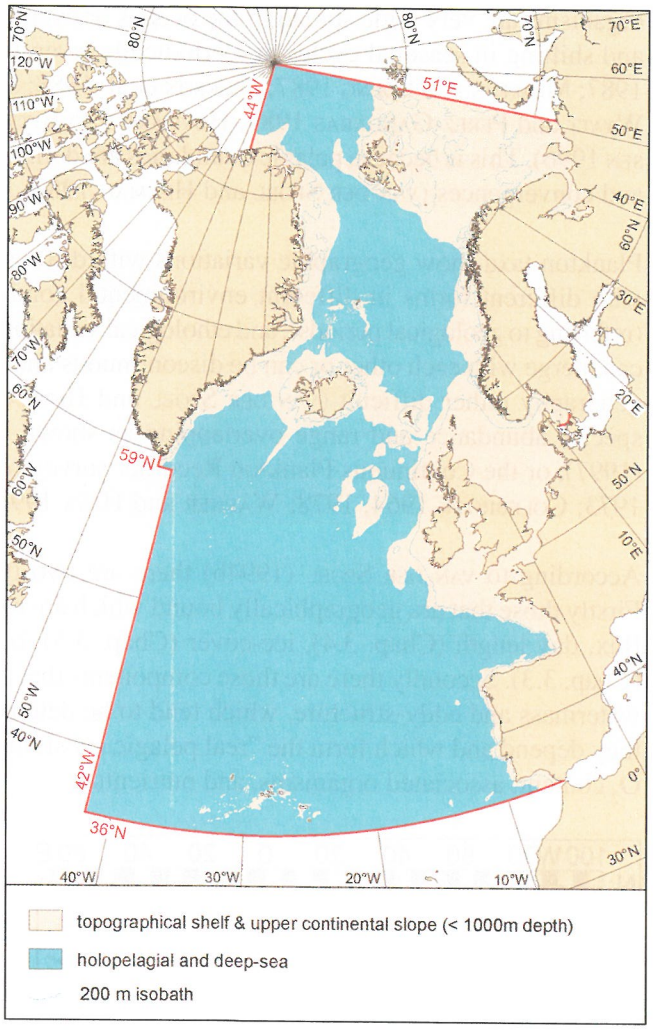


Fig. 91: neritic and oceanic areas of the OSPAR Maritime Area.

While the exact depth boundaries may differ amongst the different biogeographers, methods, taxonomic groups, and regions a lot of evidence has been published using the 1000 m isobath for a delimitation between shallow water species and influences and organisms of the deep-sea for both regions to the north and south of the Greenland-Iceland-Faeroe Rise. Thus the explanations given in the text above and in chapter 3.2 as well as the figures 82-90 and additional references (*e.g.* GRASSLE et al. 1979; GAGE and TYLER 1991) give the justification for this vertical delimitation concerning the pelagial and at the same depth for the benthal.

6.3 Characteristics of the different biogeographical units

6.3.1 Holopelagial

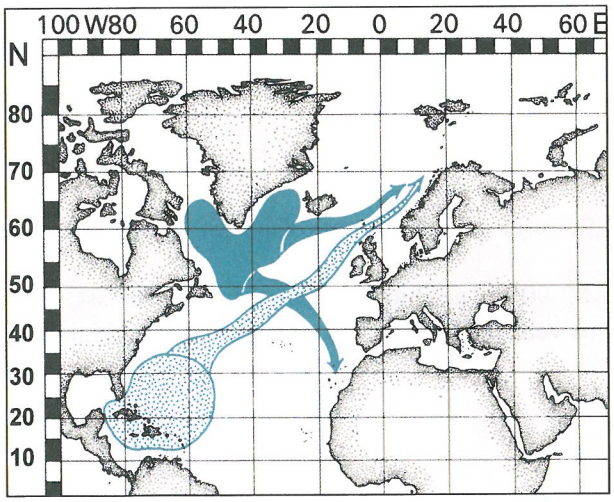
The oceanic pelagic ecosystem which is by far the largest on earth as well as in the OSPAR area shows latitudinal diversity patterns similar to other ecosystems (Fig. 104). However large scale diversity of the open ocean at a species and an ecosystem level is comparably low but it is comparatively rich at phylum level. For example, of about 14,000 marine fish species, in the Atlantic has only ~ 600 oceanic pelagial species of which are ~ 500 deep-demersal fish the rest is related to shallow and coastal waters. Local exceptions of higher diversity are typically those of boundaries between different oceanic water masses where different faunas get mixed together. These frontal zones are generally unstable and may shift seasonally by hundreds

of kilometres or alter periodically. On the other hand high species diversity in the pelagial is commonly associated with regions of low productivity that lack strong seasonality in the production cycle (ANGEL 1993).

Pelagic biogeography is often dealt with in combination with geographical patterns of productivity and biomass (*e.g.* LONGHURST 1995, 1998). Occasionally both are mixed up, but in *sensu strictu* it should reflect patterns of species distribution in space and time (Chap. 4.1). This is especially difficult since most pelagic organisms are very wide spread in the oceans or even globally, and pelagic boundaries are usually dynamic and shifting in seasonal cycles or, periodically, even fading away (*e.g.* BLINDHEIM and LOENG 1981; LOENG 1987; MIDTTUN and LOENG 1987; DICKSON et al. 1988; SKJOLDAL and REY 1989; WYATT and LARRAÑETA 1988; WYATT and PEREZ-GANDARAS 1989; HOVGÅRD AND BUCH 1990; BLINDHEIM and SKJOLDAL 1993; ANKER-NILSSEN 1996). This is because pelagic boundaries are defined mainly by water masses, frontal zones, divergences, and convergences (VAN DER SPOEL and HEYMAN 1983; ANGEL 1993).

Plankton taxa show geographic variations with different forms in different areas, ecophenotypic variations with different forms in different environmental conditions, seasonal variations, chronological variations (referring to geological periods), and ethological variations resulting in infraspecific speciation. These variations can merge with each other or can be discontinuous and thus can make taxonomic identification in relation to geography rather difficult (VAN DER SPOEL and HEYMAN 1983). In addition there are frequently sympatric species abundance and range overlapping as shown by *e.g.* VAN DER SPOEL and HEYMAN (1983), SEMINA (1997), or the Continuous Plankton Recorder survey (*e.g.* HARDY 1956, 1958, 1971a, b; LUCAS and GLOVER 1973; COLEBROOK 1964, 1978; WARNER and HAYS 1994).

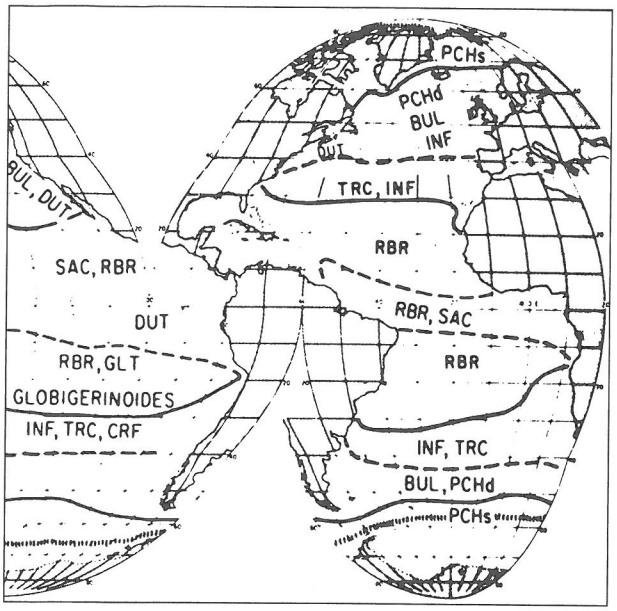
According to VAN DER SPOEL (1994b) there are two types of abiotic component in each pelagic biotope. Firstly those that are geographically bound which are relatively stable and predictable including solar energy flux, day length (Chap. 3.4), ice-cover (Chap. 3.5), bottom topography (Chap. 3.2), and current direction (Chap. 3.3). Secondly there are those components that are geographically independent and that shift with the watermass and eddy-structure, which tend to be determined by the hydrodynamics of the system on which they depend and which form the "real pelagic substratum" including salinity, temperature (Chaps. 3.3; 3.4), O_2 content, associated organisms, and nutrients.



dotted = warm-water populations
dark = cold-water populations

Fig. 92: Example for long-range expatriation in diatoms (from VAN DER SPOEL and HEYMAN 1983, clipped).

Pelagic biogeographical patterns and ranges are difficult to determine and might be misleading unless total life history of the respective species is considered due to the phenomenon of expatriation. The distribution of individual taxa show little if any coincidence with the quite sharp boundaries that emerge from analyses of communities. Pelagic species are constantly dispersed well beyond their reproductive/normal ranges by diffusion and advection in currents and meso-scale eddies into localities where they may persist but not breed. While restricted expatriation is a common phenomenon, long range expatriation also occurs, distinctly influencing the overall distributional patterns. Expatriatiated plankton can be found within its normal reproductive range, in an area where reproduction is possible, dislocated into a non-sterile expatriation area, or dispersed far beyond its reproduction possibilities into a sterile expatriation area (HAEDRICH and JUDKINS 1979; VAN DER SPOEL and HEYMAN 1983; ANGEL 1993). Expatriation areas of phytoplankton are even larger than those of zooplankton. In the NEA tropical species may drift as far as 65°/70° Northern latitude (Fig. 92) (VAN DER SPOEL AND HEYMAN 1983; SEMINA 1997).



PCHs: *G. pachyderma sinistral*
PCHd: *G. pachyderma dextral*
BUL: *G. bulloides*
DUT: *G. dutertrei*
INF: *G. inflata*
RBR: *G. ruber*
SAC: *G. sacculifer*
TRC: *G. truncatulinoides*

Fig. 93: Foraminiferal zonations in pelagic sediments. The major boundaries are markers of climatic zones: polar, subpolar, transition, subtropical, and tropical (from BERGER 1974, clipped).

Pelagic palaeobiogeography as well as sedimentology (*e.g.* for questions of palaeoclimates, palaeocirculation, palaeo-sealevels) analysing fossil records of shell bearing plankton organisms in marine sediments (Fig. 93) has to reflect the expatriation phenomenon as well as the problems of calcareous dissolution resulting from the CCD (Chap. 3.1) and therefore has to be very careful in its conclusions (*e.g.* BERGER 1974; HAQ et al. 1977; HERMAN 1979; THUNELL and BELYEA 1982; VAN DER SPOEL and HEYMAN 1983; HAQ 1984; BOLTOVSKOY 1994; OKOLODKOV and DODGE 1996).

Oceanic biogeography of pelagic assemblages matches the patterns of large-scale circulation as characterised by the distribution of water masses (*e.g.* FASHAM and ANGEL 1975; VAN DER SPOEL and PIERROT-BULTS 1979; VAN DER SPOEL and HEYMAN 1983; ANGEL 1993; SEMINA 1997) but dominant factors and factor combinations that determine distribution patterns apart from temperature still remain elusive. Individual species ranges might seldom match the water mass distribution, although community structure does show a reasonable relationship as ANGEL (1997) stated. However some water masses have a faunal assemblage associated with them, and there are some that do not. For example FASHAM and ANGEL (1975) could not find any specific assemblage related to the Mediterranean intermediate water in the NEA (comp. Chap. 3.3). Although physical mixing resulting from currents and eddies generates patchiness that may persist for months and even years, it prevents the establishment of meso-scale ecosystem diversity and may limit speciation by enhancing gene flow through advection (ANGEL 1993).

The structure and dynamics of oceanic food webs are strongly influenced latitudinally and are expressed together with species richness throughout the water column to a depth of ~ 2000 m. There is a stepped change from more continuous production conditions at subtropical latitudes over dynamic and strong mixing in temperate waters and highly seasonally pulsed production cycles at high latitudes (ANGEL 1993). These differences are related to a decrease in the duration of annual stratification from year-round layering of waters in low latitude regions over strong seasonal changes with periods of mixed isothermal conditions in Subarctic regions to permanent cold waters of the high Arctic. Prolonged periods of mixing in Subarctic regions thus prevent the establishment of species groupings within certain layers of boreal waters (VINOGRADOV 1968; VINOGRADOVA 1968; ANGEL and FASHAM 1975).
CLARKE (1992) queried the existence of a longitudinal cline in species diversity in marine communities but ANGEL (1993) and ANGEL and FASHAM (1975) demonstrated a significant cline in longitudinal diversity in a transect between 10°N and 60°N along 20°W in the NEA with a diversity peak at 18°N (Fig. 94) and an abundance peak for ostracods at 30°N. BADCOCK and MERRETT (1977) showed differences in latitudinal distribution of mesopelagic fishes between 11°N and 60°N with swimbladderless fishes by far dominating towards the south of the survey area and swimbladdered fishes showing an abundance peak at ~ 30°N.

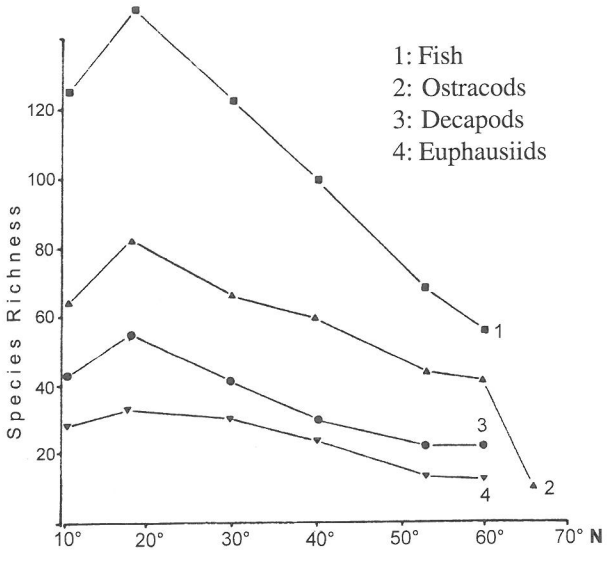
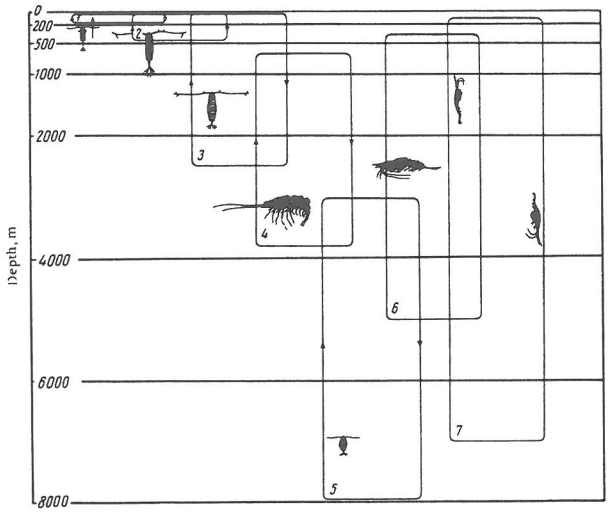


Fig. 94: Variations in the total numbers of four pelagic taxa collected in the water column to depths of 2000 m at a set of standing stations in the NEA approximately along 20°W (from ANGEL 1993).



1 - diurnal migrations encompassing the surface zone;
2 - diurnal and seasonal migrations encompassing the surface zone and the intermediate layer;
3 - seasonal and ontogenetic migrations encompassing the surface zone and the bathypelagial;
4 - ontogenetic migrations encompassing the bathypelagial and the abyssopelagial;
5 - migrations within the limits of the abyssopelagial;
6 - ontogenetic migrations encompassing the intermediate layer and a greater part of the deep-sea zone;
7 - short-term irregular (?) food migration covering almost the entire water column;

Fig. 95: Scheme of vertical migration of oceanic plankton (from Vinogradov 1968).

Pelagic species ranges are defined by environmental factors. Limiting factors can only be met by the species with an absolute reaction of either being absent or present. Other factors are tolerated for example by adaptation or by genotypic variation which creates characters that interact with the marine climate and water mass factors (VAN DER SPOEL 1994). However, PIERROT-BULTS and VAN DER SPOEL (1979) stressed the point that ecological barriers determining populations should not be confused with ecological boundaries limiting the area of optimum conditions of a species and as a consequence the area of its highest abundance. Phytoplankton seem to have even much wider distribution ranges than zooplankton, thus BEKLEMISHEV (1977) and SEMINA (1997) identified only three phytoplanktonic regions in the world ocean: arcto-boreal, tropical, and notal-antarctic.

Vertical diversity in the water column can be very high, as *e.g.* ANGEL (1991) showed with 320 species of just four taxa (fish, medusae, mysids, and ostracods) in the North Atlantic but also around half of the global inventory of *e.g.* planktonic ostracods can occur at a single locality (ANGEL 1993).

Vertical movement of pelagic organisms may be seasonal, diurnal, ontogenetic, related to feeding and self-protection, or an up- and downward move following the isotherms (Fig. 95). These vertical migrations are triggered by light, temperature, or food supply are ecologically determined. Consequently the vertical patterns are seldom stable in space and time (VINOGRADOV 1968; VAN DER SPOEL and HEYMAN 1983). In cold-water regions the seasonal vertical range of interzonal species can be very wide with the bulk of their populations inhabiting depth down to 2000-3000 m for long periods. In contrast only occasional individuals descend deeper than 1000 m in tropical regions (VINOGRADOV 1997).
With seasonal variability in solar radiation and dependant climatological features (Chaps. 3.3; 3.4; 3.5) increasing towards the north there is an increase in seasonal vertical migrations with multi-annual zooplankton lifecycles adapted to it (Fig. 95) (VINOGRADOV 1968).
Besides these seasonal vertical migrations there are diurnal/diel migrations between mixed surface and mesopelagic layers with a lower boundary of 300-500 m (700-1000 m) depth thus resulting in groups of organisms that spend day and night in different depth zones and even different water masses (Fig. 95). The intensity of vertical migration differs in species or groups of organisms (HAEDRICH and

MERRET 1988; MERRET and HAEDRICH 1997) as well as with latitude with a decrease from 30°N towards the north and south. BACKUS et al. (1977) denied mesopelagic patterns for fish in Arctic waters but MAGNÚSSON (1996) gave evidence *i.a.* for myctophid species by analysing deep-scattering layers in the Irminger Sea which is strongly influenced by the cold East Greenland current of polar origin to the west with diurnal migrations between ~450 m and ~750 m depth.
Some species even change from being non-migrant at the extremities of their range to strong migrants towards the centres (ANGEL and FASHAM 1975). In addition the diurnal vertical migration of a species might be different in different water masses. Looking at diurnal vertical migration patterns, it is difficult to determine whether zoogeographical or ecological differences are the reason (VAN DER SPOEL and HEYMAN 1983). As isothermal conditions begin to develop in northern surface waters in autumn vertical migrations become slightly longer, however the water stratification may stop them altogether in summer (VINOGRADOV 1968). Besides diurnal migrating fauna, there commonly occur expatriated or submerged organisms in those mesopelagic layers "to even more confuse the biogeographer", as LONGHURST (1998) stated. At some locations mesopelagic organisms might not even perform diurnal migrations as described by ANGEL et al. (1982). This might have been due to the situation of horizontal and vertical watermass boundaries at the location examined. In some regions some organism groups might perform diurnal vertical migrations only affecting the epipelagial, whereas others do not migrate at all as MAYCAS et al. (1999) showed.

For phytoplankton in oceanic regions the lower vertical boundary is the pycnocline because it restricts the upper mixed layer depth and therefore prevents neutrally buoyant phytoplankton cells sinking into insufficiently illuminated layers (SEMINA 1997).
Coldwater organisms show the phenomenon of polar emergence and tropical submergence in thermal étages as depicted in the chapter 3.2 and figures 13, 14. Latter figures shows different pelagic biotopes related to their vertical location due to this phenomenon in a N-S ocean cross-section (LE DANOIS 1948; ZENKEVITCH 1948/1949; EKMAN 1953; HEDGPETH 1957; DE LATTIN 1967; VINOGRADOV 1968; GLÉMAREC 1973, 1988; MENZIES et al. 1973; VAN DER SPOEL and HEYMAN 1983; VINOGRADOVA 1997; ZEZINA 1997; LONGHURST 1998;).

There are fundamental faunal differences between neritic and oceanic pelagic habitats with pronounced changes in species abundance, composition and diversity and with an inverse relationship of species richness and planktonic biomass from neritic to oceanic waters across the shelf break. It appears to be as difficult for many oceanic species to persist in inshore waters as it is for neritic species to persist in oceanic waters (HAEDRICH and JUDKINS 1979; VAN DER SPOEL and HEYMAN 1983; ANGEL 1993). Hence neritic species might show local endemisms, while very few oceanic species are endemic to such localised regions (Pierrot-Bults 1997).

Pelagic primary production is restricted to a few ten meters of the epipelagial and is represented by only ~3500-4500 phytoplankton species compared to ~250,000 of flowering plants providing terrestrial primary production (SOURNIA et al. 1991) but although productivity per area unit is lower in the ocean it accounts for a third of the annual global carbon fixation due to the huge world ocean surface (ANGEL 1993).

The trend from seasonal pulsing of production at high latitudes to more continuous production at lower latitudes (ANGEL and FASHAM 1975) related to latitudinal oceanographic differences as mentioned above is also recognisable from the figures 96-99.

Pelagic distribution and productivity patterns are mostly related to large-scale oceanographic features. LONGHURST (1995, 1998) (Chap. 5.1.13) distinguished four major pelagic biomes:
- Westerlies biome, where the mixed layer depth is forced largely by local winds and irradiance;
- Trades biome, where the mixed layer depth is forced by geostrophic adjustment on an ocean-basin scale to often-distant wind forcing;
- Polar biome, where the mixed layer depth is constrained by a surface brackish layer which forms each spring in the marginal zone;
- Coastal biome, where diverse coastal processes force the mixed layer depth.

Those biomes/regions can be differentiated du to their oceanographic characteristics (*e.g.* seasonality, mixing

versus stratification, trophic status, planktonic life cycle characteristics), but also by a quantification of thus induced plankton groups in terms of biomass.

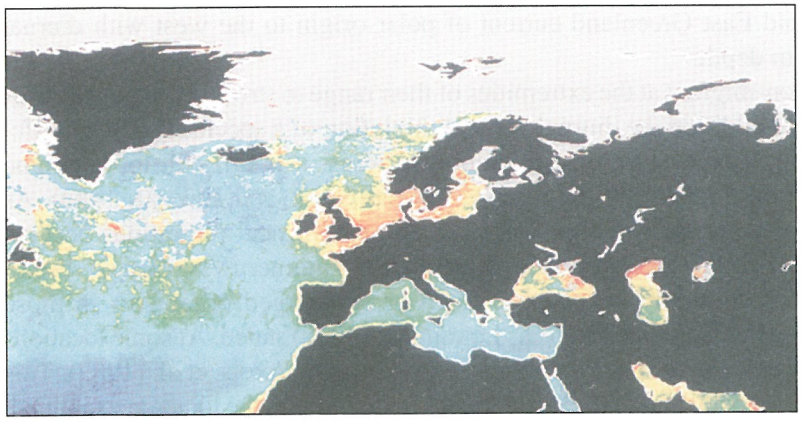


Fig. 96: Boreal winter (December-February); climatological (1978-1986) seasonal seas surface chlorophyll field obtained with Coastal Zone Color Scanner sensor (NASA/ Goddard Space Flight Centre). Color is a log scale for chlorophyll: purple = <0.06 mg Chl m^{-3}, orange-red = 1-10 mg Chl m^{-3} (from LONGHURST 1998, clipped).

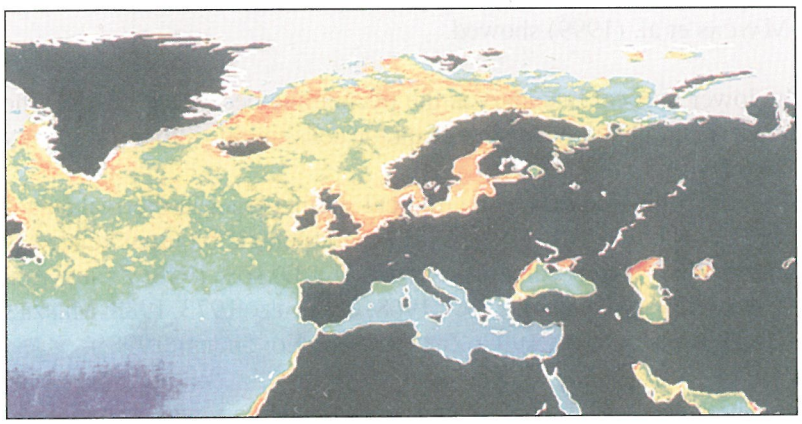


Fig. 97: Boreal spring (March-May); climatological (1978-1986) seasonal seas surface chlorophyll field obtained with Coastal Zone Color Scanner sensor (NASA/Goddard Space Flight Centre). Color is a log scale for chlorophyll: purple = <0.06 mg Chl m^{-3}, orange-red = 1-10 mg Chl m^{-3} (from LONGHURST 1998, clipped).

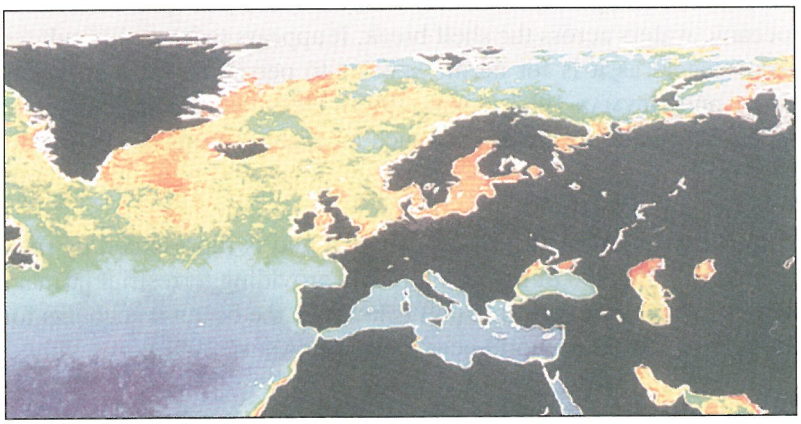


Fig. 98: Boreal summer (June-August); climatological (1978-1986) seasonal seas surface chlorophyll field obtained with Coastal Zone Color Scanner sensor (NASA/Goddard Space Flight Centre). Color is a log scale for chlorophyll: purple = <0.06 mg Chl m^{-3}, orange-red = 1-10 mg Chl m^{-3} (from LONGHURST 1998, clipped).

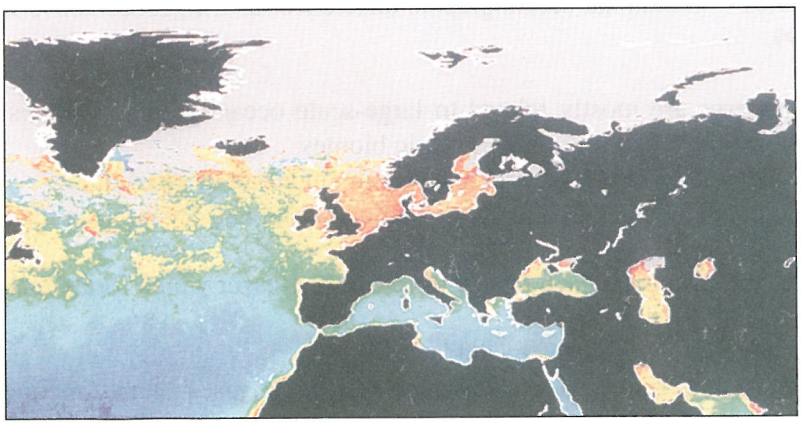


Fig. 99: Boreal fall (September-November); climatological (1978-1986) seasonal seas surface chlorophyll field obtained with Coastal Zone Color Scanner sensor (NASA/ Goddard Space Flight Centre). Color is a log scale for chlorophyll: purple = <0.06 mg Chl m^{-3}, orange-red = 1-10 mg Chl m^{-3} (from LONGHURST 1998, clipped).

The figures 96-99 (LONGHURST 1998) show the average pelagic surface productivity of the NEA and adjacent seas differentiated in four seasons received from cumulated (eight years) satellite images of chlorophyll selective spectra. Clearly visible are ice-edge related phytoplankton blooms in Subarctic waters and major trophic differences between oligotrophic permanently stratified oceanic waters south of ~45°N and northern waters of higher trophic level, influenced by fronts, upwellings, and mixing above continental shelf regions. Also observable is the influence of the Norwegian and North-Cape Currents in winter, spring and summer with a differentiation of Barents Sea waters. Not visible are the Iberian upwelling (comp. Figs. 29, 30), the Azores Front, and polynyas respectively the actual ice cover.

While the amphipods *Gammarus wilkitzkii, Apherusa glacialis*, and *Onisimus sp.* are regarded as autochthonous sea-ice associated fauna (GULLIKSEN 1984; LØNNE and GULLIKSEN 1991a, b), the copepod *Calanus glacialis* is characteristic for the pelagic **Cold Arctic Waters province** (Fig. 104). *Amphiprora paludosa* var. *hyperborea* is typical for phytoplankton in this region (SEMINA 1997). Diversity of the Greenland Sea pelagos is higher and more clearly pronounced than the one of the Arctic Basin (VINOGRADOV 1968) which is further evidence for the High Arctic Maritime province integrating a combination of pelagic and ice-cover related classification characteristics. The cluster analysis of OKOLODKOV and DODGE (1996) showed a clear distinct segregation of this province against the adjacent areas for planktonic dinoflagellates. The waters of the Norwegian and Greenland Seas were segregated from each other in species number and composition but with a closer relationship in-between the two than between the Greenland Sea and the Arctic Basin. Further characteristics of the ice-cover related cold water biotic structures have been given in chapter 3.5.

There is a geographical differentiation within the copepod genus *Calanus* with the species *C. glacialis* being typical for the high Arctic and restricted to waters north of the Polar/Arctic Fronts, *C. finmarchicus*, having the widest range, is the dominating and characteristic copepod for Subarctic (mixed Arctic and Atlantic waters – *sensu* DUNBAR) and cool-temperate regions, and *C. helgolandicus* has more affinities to warm- to cool-temperate regions, being restricted to waters south of the Polar/Arctic Fronts. *C. hyperboreus* has a distribution range within Arctic to Subarctic waters that is located between *C. glacialis* and *C. finmarchicus*. Between either of those species there are commonly areas of sympatric regional overlapping or "pseudo-sympatric" presence in different vertical layers with different properties. Populations get often expatriated *e.g. C. glacialis* south-westward by the East Greenland Current, *C. finmarchicus* southward by the Canary Current/Subtropical Gyre, and *C. helgolandicus* north-eastward by currents related to the NAD or the Mediterranean intermediate water (Chap. 3.3) (CHANG-TAI SHIH 1979; FLEMINGER and HULSEMANN 1977; VAN DER SPOEL and HEYMAN 1983; VINOGRADOV 1968). *C. hyperboreus* shows seasonal migrations over a vertical range of < 600 m while *C. glacialis* moves less than 170 m (VINOGRADOV 1997).

Many relative stenobiontic species inhabiting intermediate layers in the Norwegian sea and a whole series of oceanic Atlantic species are introduced into the Arctic basin together with the intermediate Atlantic water (±150 m to ~750-1000 m; Chap. 3.3). In this layer species abundance of the plankton is higher than in layers above or below it. The enrichment of Arctic basin fauna associated with the inflow of these waters is not limited exclusively to this layer. Most of the species of Atlantic water origin ascend into the layers of upper intermediate waters (300-100 m) or even above this to the 100-50 m layer. Another group of species inhabiting the layer of Atlantic waters descends to the deeper mixed intermediate waters in the Nansen Basin, where many of them have maximum numbers. Of these many are endemic to the Arctic Ocean or even the Nansen Basin, such as *e.g. Pseudochirella spectabilis, Chiridiella reducta, and Scaphocalanus polaris* (VINOGRADOV 1968).

The main difference between the tropical to warm-temperate regions and the cool-temperate to Subarctic regions is the sharp seasonal variation of external conditions (intensity of solar radiation, temperature, and water stratification) in later regions, while in the former such conditions vary negligible. The same factors are responsible for the differences in species composition, life cycles, ecology, vertical distribution, and trophic relationships (VINOGRADOV 1968).
FASHAM and FOXTON (1979) identified 14 groups of decapods on a transect along 20°W between 11°N and

60°N. They discriminated a major pelagic boundary at ~46°N (53°N) which correlates well with the delimitation between the **Warm-temperate** and **Cool-temperate provinces** given in this study.
VAN SOEST (1979) highlighted watermass boundaries being pelagic biogeographic barriers and indicated boundaries at ~70°N separating polar from northern temperate/Subarctic surface waters and at ~45°N separating Subarctic from subtropical surface waters in the eastern ocean basins. These definitions matches the pelagic boundaries of this study as well. BEKLEMISHEV (1977) and SEMINA (1997) distinguished phytoplankton regions of the world with a boundary between their tropical and the arcto-boreal region as well at the latitude of the English Channel entrance. North of this boundary there is a zone of mixing of tropical and arcto-boreal species reaching to south Iceland and south-west Norway.

The mesopelagic fish classification of BACKUS et al. (1977) (Chap. 5.1.11) differs from the overall pelagic classification given in this study mainly in discriminating an Atlantic Subarctic region and province which was characterised by a strong seasonality, most significant in solar radiation, much colder waters, and a southern boundary following the oceanic Polar Front of DIETRICH (1964). On the other hand no myctophid species are restricted to this region and those species living there also live in the adjacent temperate seas. The main difference between these two mesopelagic regions are a very low diversity with *Benthosema glaciale* covering 96% of all myctophid species in the Atlantic Subarctic region but a much higher productivity compared to the North Atlantic Temperate region.

According to (VINOGRADOV 1968) the winter convection in the far north Atlantic extends to a depth of 1000 m without reaching the cold demersal waters from the Norwegian Sea. The shifting stratification of northern surface waters and the prolonged periods of completely isothermal conditions prevent the establishment of groupings of species associated with certain limited layers of the surface zone (VINOGRADOV 1968). He indicated a southern boundary for his temperate-subarctic region, which comprises Arctic, northern transitional, and Boreal biologic regions, at 40-45°N.

Despite having drawn different boundaries for their mesopelagic classification BACKUS et al. (1977) argued that most of the myctophid fishes of the North Atlantic Temperate region either live in the Atlantic Subarctic or the North Atlantic Subtropical region. This differentiation is also evidence for and matches the delimitation between a Cool-temperate Waters province and a Warm-temperate Waters province given in the classification of this study with the temperate water provinces depicting also a region of gradual change and biotic transition (Fig. 104). With regard to the mesopelagial, the temperate region cools much more rapidly with depth, it is less saline, and productivity is much higher due to a complicated interplay of seasonal changes in the vertical stability of the upper part of the water column, in wind, and in solar radiation (Chap. 3.4) compared to the adjacent subtropical region (BACKUS et al. 1977). Their Azores-Britain province shows marked differences between the north-eastern and south-western corners but with no apparent physical or faunal boundary in-between thus marking a gradual transition according to the surface and near-surface flow of the NAD (Chap. 3.3).

OKOLODKOV and DODGE (1996) presented maps of the distribution of the planktonic dinoflagellates *Ceratium arcticum* and *Dinophysis norvegica* that closely match the area of the cool-temperate waters province with a southern boundary at the latitude of the English Channel.
It has been suggested that the life history of *Calanus finmarchicus* is adapted to exploit the slope current along the shelf-break to the west of Britain so that it maintains its position in the NEA (ANGEL 1997).

VAN DER SPOEL and HEYMAN (1983) showed maps with the distribution of *Coccolithus pelagicus, Limacina retroversa* forma *retroversa, Nitzschia cylindrica,* as well as of the humpback whale *Megaptera noveangliae*, that approximately match the area or boundaries of **Cool-temperate waters** as distinguished in this study (Fig. 104). LUCAS and GLOVER (1973) showed maps with the distribution of *Euchaeta norvegica* that give further evidence for a delimitation of this province. *Ceratium arcticum* and *Coscinidiscus oculus-iridis* as Arcto-Boreal species have their southern boundary at the English Channel as well as *Ephemera (Navicula) planamembranaceae* according to SEMINA (1997). Latter species, as a being a Boreal-Atlantic species, has a northern boundary at south-Greenland, south Iceland, and south-west Norway.

Warm-temperate waters comprising the Boreal-Lusitanean province with the warm water western approach of the British Isles were shown by VAN DER SPOEL and HEYMAN (1983) or LUCAS and GLOVER (1973) as inhabited by the plankton species *Peraclis reticulata, Pterotrachea spec., Rhizosolenia bergonii*, whereas the entire temperate provinces have been characterised by *Diacria trispinos atlantica and Sagitta tasmanica.*

VAN DER SPOEL and HEYMAN (1983) showed maps with the distribution of *Histiotheuthis bonelli, Eucalanus hyalinus, Pulleniatina obliquiloculata, Thysanoessa gregaria, Euphausia americana, Sagitta serratodentata serratodentata,* that approximately match the area or boundaries of **Warm-temperate waters** as distinguished in this study (Fig. 104). The subspecies *Sagitta serratodentata atlantica* has a distribution comprising the warm-temperate pelagic province including the neritic Boreal-Lusitanean province as northern boundary according to PIERROT-BULTS (1997). The same applies to *Planktoniella sol* (SEMINA 1997).
LUCAS and GLOVER (1973) showed maps with the distribution of *Euchaeta acuta* that give further evidence for a delimitation of this province. According to PIERROT-BULTS and VAN DER SPOEL (1979) the *Eucalanus elongatus* group has its northern boundary exactly at the northern delimitation of the warm-temperate province of this study.

The mesopelagic Mediterranean Outflow province of (BACKUS et al. (1977) is characterised by the dominating area of intrusion and strongest influence of warm (10°C) and high salinity (35.7‰) water between upper Atlantic mixed water and North Atlantic deep water or Labrador water respectively (Chap. 3.3, Figs. 25-28).
Regarding the **bathypelagial**, maps from VAN DER SPOEL and HEYMAN (1983) show the distribution of *Cyclothone pseudopallida, C. atraria* and *Limacina helicoides* as being characteristically for the **deep North Atlantic province** (Fig. 107) south of the Greenland-Scotland ridge system. For demersal fish the fauna off Iceland, the Norwegian Basin, and the Rockall Trough in archibenthal/bathyal depths were very similar (HAEDRICH and MERRET 1988; MERRET and HAEDRICH 1997).
According to the general tendency of deeper waters to increase uniformity with depth there are more species with wide distributions in the bathypelagial, partly showing tropical submergence, and in the abyssopelagial (VAN SOEST 1979).
At **abyssopelagial** depths of > 2700 m the same water mass of North Atlantic deep water is ubiquitous with several faunal elements being also ubiquitous (ANGEL 1993).

6.3.2 Benthal and Neritopelagial of the Shelf and Upper Continental Slope and Ice-Cover biomes

Reasons and evidence for joining the shelf with the upper continental slope for this biogeographic realm of this classification have been given in chapter 6.1.

For a correspondence of the neritopelagial with the "shallow" benthal delimitations there was given further evidence by BRIGGS (1995) who considered the continental shelves to be one unit of the benthic realm together with the overlying neritic water column and VAN DER SPOEL and HEYMAN (1983). Later authors presented a map with a delimitation of the neritopelagial according to their "distant-neritic" concept. This map shows neritic distribution ranges reaching far beyond the shelf break, also to about the 1000 m isobath. This closely match the delimitations given in the classification of this study. For the OSPAR area they showed nearly the same boundaries between North-East Greenland and South-East Greenland, the Warm-temperate and Cool-temperate waters/Lusitanean-Boreal and Boreal-Lusitanean provinces, the Skagerrak and West Norwegian subprovinces, and the West Norwegian and Finnmark subprovinces.

The role of sea-ice as a substrate being comparable and partly closely related to the benthal has been described in the chapters 3.5 and 3.5.1 and is thus regarded also by pelagic biogeographers as *e.g.* VAN DER SPOEL and HEYMAN (1983).

Temperate water masses:
According to EKMAN (1953) and SEMINA (1997) the Warm-temperate (Lusitanean) and Cool-temperate (Boreal) provinces lack a truly epipelagic endemic fauna thus being populated mainly by cosmopolitan species. This oceanic holopelagic uniformity gets more divers and specific in neritic regions.

Similar to the pelagial, there is a latitudinal cline of species diversity away from the equator on continental shelf areas. For instance CHRISTIANSEN (1982) pointed out the existence of 200 brachyura crab species along West African coasts, 112 species at the Iberian peninsula, 47 species north of the English Channel, 31 species along the Norwegian coast, and only 2 species penetrating into the Spitzbergen/Svalbard area.
Apart from this latitudinal cline there are areas of higher biodiversity in regions of transition where species which have their centre of distribution elsewhere are still able to survive and reproduce in the periphery of their range enriching local biocoenoses. Additionally, a variety of habitats (soft and hard substrates, mixed and stratified waters, fronts) enriches local diversity of marine species. Such areas of enhanced marine biodiversity are *e.g.* in the western English Channel and the whole transition area between warm-temperate/ Lusitanean organisms and cool-temperate/Boreal organisms on the West-European shelf between the Gironde estuary and NW-Scotland (Lusitanean-Boreal and Boreal-Lusitanean provinces) and the transition zone between Boreal and Boreal-Arctic forms from about the Shetland Islands to the middle of the Westnorwegian subprovince (from the Hardangerfjord to Haltenbank).

SCHOPF et al. (1978) argued that the correlation between species diversity and shelf area would improve if only the habitable shelf area was used while the proportion of shelf habitats suitable for certain benthic organisms varies with latitude. These considerations apply to much of the North Sea and the French Atlantic coast south of the Gironde estuary, where soft substrates dominate and ratios for in- and epibenthic fauna and macroalgae differ considerably from hard substrate areas of the same latitude and oceanographic regime.

EKMAN (1953) and VAN DEN HOEK and DONZE (1967) concluded that "no effective barrier to distribution is to be found along the European coasts and therefore sharply defined limits obviously cannot be expected. The Boreal province was therefore supposed to be bounded by intermediate zones with representations from both neighbouring faunas.

A sharp break in trophic relationships from stable to seasonal productivity at ~45°(40°)N on the other hand results in a similar decline in species as highlighted by TAYLOR and TAYLOR (1977) for gastropods. This change in seasonality is encountered by different feeding strategies changing from specialised behaviours of gastropods in stable (sub)tropical conditions to opportunistic feeders in high latitudes (TAYLOR and TAYLOR 1977).

Units of warm-temperate water masses:
Due to current patterns (Chap. 3.3) and long intercontinental distances the Atlantic ocean acts as a distribution barrier for many benthic shelf and neritic species. This has resulted in a pronounced oceanic character of the **Azores subprovince** with a comparably low diversity and few endemics. **Macaronesia** in a wider sense includes the Cape Verde, Canary, Madeira, Salvage Islands and archipelagos (for some authors also a stretch of the west African coast), and the more isolated Azores, being the only part of Macaronesia situated within the OSPAR area.
LLORIS et al. (1991) regarded the Macaronesian region as an ichtyofaunistic crossroad, where amphiatlantic, circumglobal, and cosmopolitan species merge with a northern ("septentrional") group (Boreal, Atlanto-Mediterranean, Endemics) and a southern ("meridional") Equato-Guinean group. This picture of Macaronesia as a biogeographic meeting point was confirmed by SANTOS et al. (1995) although later authors criticised an incorrectness in the database of former authors. Within Macaronesia the Cape Verdean Islands do show already a markedly higher tropical character while the Azores have a somewhat impoverished biodiversity with a more oceanic character (TÜRKAY 1982; PRUD'HOMME VAN REINE and VAN DEN HOEK 1988; LLORIS et al. 1991).

Nevertheless PRUD'HOMME VAN REINE 1988; PRUD'HOMME VAN REINE and VAN DEN HOEK (1990, Chap. 5.1.16), LLORIS et al. (1991, Chap. 5.1.15), and SANTOS et al. (1995) came to the conclusion that waters around the Azores show the poorest species representation compared to adjacent regions and have very few endemics. This restricted diversity might possibly be due to their geographical and oceanographical isolation and only a very narrow fringe of shallow waters hindering colonisation of the island's margins by littoral organisms. The drop of sea temperatures during the Pleistocene is believed to have resulted in a mass extinction with a

too short period for species differentiation after recolonisation (SANTOS et al. 1995). Despite the fact that dominant surface current patterns reach the Azores from the west, littoral fauna and flora show affinities with the eastern Atlantic coasts. Intermediate waters of Mediterranean origin (Fig. 25-27), together with a chain of seamounts and small islets between the Azores and the African coast, large scale eddies, and the topographic features of the Portugal-Azores rise (Fig. 10) could have provided stepping-stone patterns for a spreading of Lusitanean/Mediterranean species (SANTOS et al. 1995), while surface current patterns (Fig. 15) – approaching the Azores mainly from the west (GOULD 1985; KLEINE and SIEDLER 1989; SANTOS et al. 1995) – depict a hurdle for species dispersal due to great distances separating the Azores from the American coasts.

The Azores therefore are regarded as a subprovince with a more temperate character and with a closer affinity to Madeira within the Macaronesian province which again seems to be quite separated from the Lusitanean province described by BRIGGS (1974) or the Mediterranean.

The **Lusitanean province** has been differentiated into a **Northern** and a **Southern Warm subprovince** with a **Cool subprovince** in-between.
BRIGGS (1974) set out endemism rates of ~ 40% for echinoderms and ~ 50% for fishes for the whole Lusitanean (warm temperate Mediterranean-Atlantic) province and VAN DEN HOEK (1975) gave ~ 40 % for seaweeds.

The figures 29, 30 as well as the "Times Atlas and Encyclopaedia of the Sea" (COUPER 1989), show high phytoplankton productivity at the **Cool Lusitanean subprovince** which is characterised by moderate seasonal upwelling of cold water during summer months and related nutrient enrichment of coastal waters off west Portugal and north-west/north Spain (Galicia, Asturias, Cantabria) (Chap. 3.3). "Northerly" macroalgae, invertebrates and lichens which otherwise do not occur south of Brittany re-appear along the coasts bathed in cool upwelled waters (LAMI 1931; FISCHER-PIETTE 1955). These summery cold upwelled waters segregate the **Warm Lusitanean subprovince** into a **southern part** along the Gulf of Cadiz and the Algarve and a **northern part** along the Basque and Aquitaine coasts (Gulf of Gascony) (Figs. 29, 30) (FISCHER-PIETTE 1957; WOOSTER et al. 1976; FRAGA 1981; FIÚZA et al. 1982; FIÚZA 1983; WYATT and LARRAÑETA 1988; WYATT and PEREZ-GANDARAS 1989; MITTELSTAEDT 1991; VAN CAMP et al. 1991; VARELA 1992; BODE et al. 1996). This seasonal variability in western and northern Iberian coastal waters has different effects on sessile benthic organisms in contrast to the mobile pelagos that might move to preferred optimum conditions. Both warm Lusitanean areas do also show a considerable proportion of sediment dominated sublittoral and coasts besides a different hydrological regime in contrast to the predominantly rocky coasts of the cool subprovince. These markedly differences have influences as well on littoral organisms as on patterns pelagic species composition and productivity. IBÁÑEZ et al. (1989) described a marked discontinuity in intertidal ichtyofauna along the northern Spanish coast related to the different hydrological regimes. Such discontinuities between the northern warm Lusitanean and the cool Lusitanean subprovinces have been described as well by SAUVAGEAU (1897); LAMI 1931, 1933; FISCHER-PIETTE and PRENANT (1956), FISCHER-PIETTE (1935, 1938, 1952, 1953, 1955, 1957, 1963), VAN DEN HOEK and DONZE (1966, 1967), and GALLARDO et al. (1985) for benthic algae, invertebrates, and lichens. Above that IBÁÑEZ et al. (1989) accentuated an increase in diversity and southern species abundance towards the Basque coast in contrast to a low diversity in the upwelling influenced regions of Galicia and Portugal.

Another striking difference is the different current regime during the winter half-year in this region with local circulation patterns altering the oceanographic constellation. While facing cool upwelling waters during the summer there flows a warm coastal current around the Iberian peninsula from Portugal to the inner Bay of Biscay up to the Basque country on the other hand (FROUIN 1990) (Fig. 15). In addition, there is a patchwork of different water masses on the northern Bay of Biscay shelf. Surface/coastal waters are seasonally and locally influenced by a near coast warm water tangue in autumn and cool and locally fresher water masses with an inverted stratification in winter as described in chapter 3.3 (PINGREE and LE CANN 1990; KOUTSIKOPOULOS and LE CANN 1996). These give further evidence for a differentiation between the **Northern Warm Lusitanean** and the **Lusitanean-Boreal (sub)provinces**.

There are several rías and submarine canyons indented into the Iberian continental slope as well as multiple seamounts off the Iberian coast partly reaching with their summit into shallower depths of the Lusitanean waters (Chaps. 3.1; 3.2). Only poor knowledge exist about the biogeographic relations and entire vertical zonation of these topographic features. ROUX (1985) described an enhanced diversity of crinoids and abundance at greater depths in this region due to the seasonally increased nutrient input which is caused by upwelling waters.

The distribution of benthic species along the French Atlantic coast was described and mapped *e.g.* by FISCHER (1943) and CRISP and FISCHER-PIETTE (1959). Former authors had given a list of northern organisms with southern distribution boundaries and southern organisms with northern distribution boundaries along the French Atlantic coast, whereas Evans (1957) focused on the vertical zonation of the littoral fringe along the Atlantic coast of France. Many northern boreal and even boreal-arctic forms are known to occur submerged at greater depths in the Bay of Biscay where some of them have their southern distribution boundaries (BOUCHET and WARÉN 1979; ROUX 1985; GLÉMAREC 1998, 2000/pers.com.).

The **Lusitanean-Boreal province** is additionally characterised by the stationary "bourrelet froid" water mass and an influence from warm water masses, derived from the NAD, overflowing the broad continental shelf and taking part in the formation of the Ushant (Ouessant) Front west/north-west of Brittany (Chap. 3.3, Figs. 10, 15) (PINGREE 1993; PINGREE et al. 1975; PINGREE et al. 1976). Marine biodiversity is high due to a wide variety of soft and hard substrate habitats and due to the situation of being a region of transition where southern Lusitanean and northern Boreal species merge.

South of the Gironde estuary there are predominantly soft substrates which cause a major change in the character of marine biocoenoses. Thus the boundary between the warm Lusitanean and the Lusitanean-Boreal provinces is also one of a different benthic substrate. Some biogeographers regard the differentiation between those two provinces as an artefact (DAUVIN 1997; GLÉMAREC pers. com.) but due to the actual large scale differences in marine life it might be justified to reflect these differences also in this classification.

Further evidence for a discrimination between both provinces had been given by SOUTHWARD (1979, 1985), who described a clear faunistic difference and a discontinuity in the presence of Pogonophora species between the shelf margins and upper continental slopes of the northern Bay of Biscay, Celtic and Hebridean shelves (Lusitanean-Boreal and Boreal-Lusitanean provinces) and those of the southern Bay of Biscay and Portugal (Lusitanean province). Similar differences concerning echinoderms have been described by SIBUET (1977). The brachyura crab *Hyas coarctucs* as being a cool-temperate indicator has been recorded as far southwards as to the French Gironde estuary (CHRISTIANSEN 1982).

VAN DEN HOEK and DONZE (1967) emphasised the outstanding species richness of the algal floras of NW-Spain and NW-Brittany which might be caused by the abundance of species related to different water masses. Thus different biota meeting at these localities enhance diversity and give evidence for biogeographic boundaries in these areas.

FORBES and GODWIN-AUSTEN (1859) stressed the presence of Lusitanean forms around the Channel Islands which were absent from the south-western coasts of England and FISCHER-PIETTE (1936) described the biocoenotic difference on either side of the western English Channel. CRISP and SOUTHWARD (1958) gave a detailed description of the biogeographic boundary situation for invertebrates and macroalgae in the English Channel. The main difference is between the warmer, slightly more saline western basin with less extreme variations and the impoverished eastern (Boreal) basin where many southern warm-temperate/Lusitanean species fail to penetrate into. The other delimitation is between the warmer French (Lusitanean-Boreal) and the slightly cooler English (Boreal-Lusitanean) coasts of the western English Channel basin. Others (EKMAN 1953; HOLME 1961, 1966; CABIOCH 1968; BEKLEMISHEV 1977; CABIOCH et al. 1977; FLEMINGER and HULSEMANN 1977; MICHANEK 1979; PIERROT-BULTS and VAN DER SPOEL 1979; EARLL and FARNHAM 1983; HAYDEN et al. 1984; GOLIKOV et al. 1990; BRIGGS 1974, 1995; GUBBAY 1988, 1995a; OKOLODKOV and DODGE 1996; SEMINA 1997; HISCOCK 1985, 1991, 1998) confirmed this phenomenon which might underline a biogeographic

delimitation between the warmer **Lusitanean-Boreal province** and the cooler **Boreal-Lusitanean province** in the western English Channel and a further delimitation against the **Boreal province** having its south-western boundary in the eastern English Channel (Figs. 104, 105, 106).
Even for mesopelagic fish the delimitation between the Mediterranean Outflow and Azores-Britain provinces had been given approximately at the area/latitude of the western English Channel entrance/Brittany by BACKUS et al. (1977) (Chap. 5.1.11; Fig. 16).

Biogeographic changes within the NEA temperate region have otherwise a more continuous character, as indicated by the continuously graduated colour range in the figures 15, 104 (related to surface temperatures). Along the western and southern coasts of the British Isles up to the Orkney-Shetland channel sublittoral biota do show pronounced Lusitanean affinities (EARLL and FARNHAM 1983; MITCHELL et al. 1983; GUBBAY 1995; HISCOCK 1985, 1991, 1998). CRISP and SOUTHWARD (1958) and GUBBAY (1988) have published lists of species associated with areas of distinct marine climate regimes or having their distribution boundary around the British Isles.

Units of cool-temperate water masses:
According to CHRISTIANSEN (1982) the brachyopods *Hyas araneus* and *H. coarctucs* might be indicators for cool-temperate shelf provinces having a distribution range from shelves south of England (north of the French Gironde estuary) to north of Spitzbergen and the western Barents Sea.

The "Times Atlas and Encyclopaedia of the Sea" (COUPER 1989) also included the Boreal-Lusitanean province and the south-eastern North Sea in its Atlantic warm temperate marine biogeographic area. This boundary in the western English Channel correlates also with the one given by ZEZINA and VINOGRADOVA (1998) with brachiopods for the benthic realm of the shelf and continental slope. Warm waters deriving from the NAD (Fig. 15) characterise the **Boreal-Lusitanean province** (Figs. 105, 106) with its broad Celtic shelf (Fig. 10) and warm water species are able to appear at comparable high latitudes to the west of south-west England, Ireland, and Scotland. Thus, this province is also an area of enhanced marine biodiversity and of transition as shown by EARLL and FARNHAM (1983) and MITCHELL et al. (1983) with an decreasing south to north gradient in southern warm-temperate (Lusitanean) forms. CHRISTIANSEN (1982) highlighted the number of 60 brachyura crab species if the south and west coast of the British Isles are included *versus* a number of 47 species occurring otherwise north of the English Channel in the NEA. Scottish sea lochs are richer in many species groups, sublittoral communities, and habitats compared to south-western Norwegian fjords as revealed by CONNOR (1991).

A biogeographic discontinuity between Clare Island and the Faeroes was stressed by EARLL and FARNHAM (1983) (Chap. 5.1.5) on the base of data of VAN DEN HOEK (1975) (Chap. 5.1.16). According to VAN DEN HOEK (1975) and VAN DEN HOEK and DONZE (1967) this region is an area of transition where many southern species reach their northern limit and a considerable number of northern species also reach their southern limit with a comparatively low endemism rate of ~11% for cold-temperate seaweeds. The phytogeographical boundary between the cool-temperate/Boreal and the warm-temperate/Lusitanean (Lusitanean-boreal) provinces to the west of the British Isles drawn by *e.g.* VAN DEN HOEK and DONZE (1967), VAN DEN HOEK (1975), MICHANEK (1979), LÜNING (1985), and PRUD'HOMME VAN REINE (1988) lies in-between those boundaries described for faunal patterns in the Faeroe Channel, respectively Orkney-Shetland Channel, and in the English Channel (*e.g.* BACKUS et al. 1977; BRIGGS 1974; GUBBAY 1995; HISCOCK 1998).

The Shetland-Orkney channel represents both a northern and eastern boundary for many southern species with many species not being found in other locations in the North Sea (EARLL and FARNHAM 1983; GUBBAY 1988; HISCOCK 1985). An even much stronger boundary is the Faeroe channel. Rather complex current patterns separate cold water, cool temperate-boreal, and warm temperate water related organisms within a comparatively small geographical area between the Faeroe shelf on the one side and the shelf around the Shetlands, Orkneys, and the northern Scottish tip together with the Wyville-Thomson Ridge, Bill Bailey's and Faeroe Bank on the other side (MEINCKE 1983; WESTERBERG 1979). To the south the Celtic/Scottish shelf, Anton Dohrn and Hebrides Terrace Seamounts, Rockall Plateau, the Porcupine, Hatton, Lousy, George Bligh,

and Rosemary Banks are influenced at shallower depths by the warm NAD and at intermediate depths by the more warm and saline Mediterranean intermediate water masses as far as they may reach to the north (Chap. 3.3). There was also given a boundary for mesopelagic fish between their Subarctic and Azores-Britain provinces by BACKUS et al. (1977) in this area (Chap. 5.1.11; Fig. 61).

Waters of the enclosed Irish Sea tend to be colder than warm NAD-descendant currents on the Scottish/ Hebridean and Celtic shelves around. Several frontal systems develop seasonally in the Irish Sea and marked seasonally changing front systems are formed either in the North and St. George's Channel (Islay and Celtic Sea Fronts) and in the English Channel between cooler Boreal and warmer (Lusitanean) waters (CRISP and SOUTHWARD 1953; PINGREE et al. 1976; PINGREE and GRIFFITH 1978; LEE and RAMSTER 1981; SIMPSON 1981; EARLL and FASHAM 1983; CRISP 1989). Especially CRISP and SOUTHWARD (1953), SOUTHWARD and CRISP (1954), and CRISP and KNIGHT-JONES (1955) pointed out differences in the distribution of intertidal organisms related either to Lusitanean character on the western approaches or Boreal character within the Irish Sea. BEARDALL et al. (1982) and DICKEY-COLLAS et al. (1996) described distinct differences in the mix of plankton species found on either side of the Western Irish Sea Front whereas REES and HOPE-JONES (1982) and BEGG and REID (1997) described implications and patterns of seabirds associated with frontal systems in the Irish Sea and HOLME. REES (1986) revealed a high benthic diversity enrichment below the Western Irish Sea Front.

Although biogeographic differences between the Irish Sea and the adjacent seas might be only of minor character there had been given evidence for the incorporation of the cooler Irish Sea into the **Boreal province** and a delimitation against the **Boreal-Lusitanean province** by CRISP and SOUTHWARD 1953, 1954; SOUTHWARD and CRISP 1954; CRISP and KNIGHT-JONES 1955; PINGREE and GRIFFITH 1978; SIMPSON 1981; CRISP 1989; GUBBAY 1995; HISCOCK 1998; ELLIS et al. 2000/in press, and many species distribution maps of VAN DER Spoel and HEYMANN 1983. MACKIE (1990) and MACKIE et al. (1995) described benthic communities in the Irish and adjacent Celtic Sea with a differentiation to substrate types and confirmed the Lusitanean influence to the south of the Irish Sea.

Shelf-break and tidal front systems (*e.g.* Islay, Western Irish Sea, Celtic Sea, Scilly Isles, and Flamborough Fronts) around the British Isles and their biological implications had been described by *e.g.* CRISP and SOUTHWARD (1953); SOUTHWARD and CRISP (1954); CRISP and KNIGHT-JONES (1955); LEE (1970); PINGREE et al. (1974); PINGREE et al. (1975); PINGREE et al. (1976); SIMPSON et al. (1977); PINGREE and GRIFFITHS (1978); SIMPSON et al. (1978); HOLLIGAN (1978, 1981); LEE AND RAMSTER (1981); SIMPSON (1981); BEARDALL et al. (1982); REES and HOPE-JONES (1982); CRISP (1989); PINGREE (1978, 1993); DICKEY-COLLAS et al. (1996); BEGG and REID (1997); LONGHURST (1998), whereas REES et al. (1999) made a recent comparison of benthic diversity in the North Sea, English Channel, and the Celtic Sea.

The **Boreal province** consists of the North Sea with adjacent shelf areas north of Scotland, the eastern English Channel, and the Kattegat. The main current of the North Sea, a branch derived from the NAD/ Norwegian Current, enters the North Sea north of Scotland and runs through the North Sea in a counter clockwise direction (Fig. 15) with tides swelling around three amphidromic centres. The enclosed nature of the North Sea and the Irish Sea with their retained water bodies result in limited water exchange, greater seasonal fluctuations with lower winter temperatures compared to open oceanic areas, and different nutrient (and pollutant) dynamics with resulting implications on marine diversity and productivity.
Descriptions of benthic macrofaunal communities of the North Sea have been given *i.a.* by GLÉMAREC (1973), SALZWEDEL et al. (1985), BASFORD et al. (1990), REISE and BARTSCH (1990), KRÖNKE (1992), and KÜNITZER et al. (1992),.

Current patterns in the Skagerrak and Kattegat are complex. On the southern side of the Skagerrak there is a current of higher salinity entering the western side of the Kattegat from the North Sea around the Jutland peninsula, while on the eastern side of the Kattegat salinity gets reduced by the brackish Baltic Current which merges with deep saline Atlantic water upwelling from the Norwegian Deep trough on the northern side of the Skagerrak (Skagerrak subprovince of the Norwegian coast province) (Figs. 15, 18).
The southern coast of the North Sea is characterised by the tidal Wadden Sea with its special ecological

conditions (WOLFF 1983; REISE and BARTSCH 1990; BEUKEMA 1992; LOZÁN et al. 1994).
The southern subprovinces of Norway and the South Iceland-Faeroe province, as delimited in this classification, have close affinities to the character of the Boreal province (*e.g.* as classified by EARLL and FARNHAM 1983) but still have peculiarities that make them different as described below. A segregation of those provinces depends on the scale of biogeography and criteria for the classification. The record table of NEA cool-temperate brachyura of CHRISTIANSEN (1982) seems to be a valuable tool for an identification and segregation of the Boreal provinces as classified hereby from other adjacent Boreal-Arctic and Boreal areas as *e.g.* the W-/S-Iceland, Norwegian subprovinces, the Belts, and the western Baltic Sea.

The Swedish west coast is influenced by the brackish Baltic outflow (Fig. 15). The surface water salinity commonly gets reduced to 10 ‰ by these water masses, whereas there is a deeper water layer of ~30 ‰ (HISCOCK 1998). MICHANEK (1979) described difficulties in a biogeographic delineation on the Swedish west coast in the vertical as well as in the horizontal dimension. Vertically there is an upper southern flora related to warm surface waters in the summer, while at the same time water below the discontinuity layer (~15 m) is cold and the flora has northern affinities. This would correlate with the étage concept of GLÉMAREC (1973, 1988). Horizontally there are 3-5° C higher surface temperatures inside a fringe of skerries, bays and fjords compared to the adjacent open sea on the Swedish west coast with related effects on species composition.

The special character of the **Norwegian** (and Russian Murman) **coast province** was described as incorporating a triple biogeographic gradient with one Boreal to Arctic gradient from Sweden to far beyond the Russian border and an other fully marine to freshwater thermal and haline gradient from the Norwegian Sea and the shelf through coastal sounds to inner estuarine fjord systems (Fig. 18) and from the intertidal zone to the deepest basins of fjords and the shelf (ZENKEVITCH 1963; BRATTEGARD and HOLTHE 1995). The margin off the SW-Norwegian coast is separated from the rest of the European continental shelf by a trough, the Norwegian Deep, which originates in the Skagerrak and sweeps northward parallel to the Norwegian shore (Figs. 10, 91) (GROOMBRIDGE and JENKINS 1996). BRATTEGARD and HOLTHE (1995) differentiated Atlantic, coastal, and brackish water masses with related and partly variable currents and seasonally shifting isohalines which together characterise the Norwegian coast. Typically, deep Atlantic saline water flows over a sill into deep fjord basins, whereas a brackish surface layer merges with saline water and mixes with water masses of the Norwegian coastal current, which is a continuation of the brackish Baltic current. The saline Norwegian current of NAD origin and the brackish Norwegian coastal current merge towards the north (Fig. 15) (BLINDHEIM and LOENG 1981; BRATTEGARD and HOLTHE 1995). A vertical border between the Atlantic-Boreal and Arctic biogeographical regions lies at depths of 30-40 m in the Norwegian fjords according to GOLIKOV et al. (1990). The present marine fauna was established after the last deglaciation with an immigration of boreal forms and a retreat of cold-water Arctic forms along the Norwegian coast with cold- and warm water relics being distributed in disjunct patterns and "endemics" being regarded as artefacts (EKMAN 1953; BRATTEGARD and HOLTHE 1995, 1997; GUBBAY 1995).
The region from the Hardangerfjord to Haltenbank within the **Westnorwegian subprovince** is a transition area with a high biodiversity and where Boreal and Boreal-Arctic forms both occur (BRATTEGARD and HOLTHE 1995). The Westnorwegian and Finnmark subprovinces were indicated by COUPER (1989) to have a high production with an extraordinary high Phyto- and Zooplankton biomass. The record table of NEA cool-temperate brachyura of CHRISTIANSEN (1982) seems to be another valuable tool for the delimitation of the different Norwegian coast provinces and a segregation from other adjacent Boreal-Arctic and Boreal areas as W-/S-Iceland, Shetland, North Sea, and Kattegat.

CONNOR (1991) revealed that south-western Norwegian fjords are less rich in species, sublittoral communities, and habitats due to a smaller tidal range and low salinity conditions compared to Scottish sea lochs, although fish, bryozoans, sponges, and calcareous tubeworms are better represented in Norwegian fjords.
The complete absence of the Arctic sea urchin *Echinus acutus* in British waters which, on the other hand, is abundant in shallow depths in south-west Norway and the extreme abundance of *Strongylocentrotus droebachiensis* in Norway compared to isolated populations of Shetland underline the biogeographical difference (BRATTEGARD and HOLTHE 1997; HISCOCK 1998). But there were also described the southern (Lusitanean) forms *Octophialucium funerarium*, *Upogebia sp.*, and especially *Palinurus elaphas* in SW-

Norwegian waters (TAMBS-LYCHE 1958) which might be related to the flow path of Atlantic water masses of the NAD/Norwegian Current system flowing along the (Boreal-Lusitanean) west British shelves and before approaching SW-Norway (Fig. 15). The Norwegian Deep channel might be a deep-water pathway for eurythermic Arctic-boreal species, where they can migrate "submerged" as far to the south as the Skagerrak (BRIGGS 1974).

Although being dominantly of cool (cold) temperate (boreal) character and showing many similarities with the South Iceland-Faeroe Shelf and northern Boreal provinces, there have been adopted the subdivisions of BRATTEGARD and HOLTHE (1995, 1997) for the Norwegian Coast province in this study, even if the subprovinces seem to be of a comparably detailed level. Other biogeographers include the whole Norwegian coast together with southern Iceland and the Archipelagos in-between in a Boreal-Arctic (HISCOCK 1998) or cool temperate (GLÉMAREC 1998/2000/pers. comm.) province which might be also acceptable. However a major biogeographic discontinuity had been described also at the latitude of the Trondheim fjord (~ 63°30'-65°N) (BRATTEGARD and HOLTHE 1995; CHRISTIANSEN 1982; GUBBAY 1995; GLÉMAREC 1998/2000/pers. comm.).

The **Skagerrak subprovince** reflects the brackish influence of the Baltic surface current which merges to some extent with deep saline Atlantic water that wells up from the deep Norwegian trough. According to HELA and LAEVASTU (1961), SHERMAN and ALEXANDER (1986), and GOLIKOV et al. (1990) this subprovince does not differ much from the adjacent Boreal North Sea areas, but, on the other hand, it contains Boreal, Boreo-Arctic, and Arctic isopod communities related to the different water masses (HULT 1941). Also occurrence of cold-seep endemics in the deep Skagerrak (GOLIKOV et al. 1997) might give this subprovince a distinct character.

The **Finnmark subprovince** along the Murman coast is characterised by a high abundance of Arctic-Boreal forms, a high tidal range (< 4.17 m), a high seasonality and meso-scale variability related to the effects of warm Atlantic and cold Barents Sea/Arctic waters that influence biological patterns especially of pelagic biota. Following a spring development of diatoms, there is a high peak in *Phaeocystis* dominated phytoplankton in May and lesser peaks conditioned by peridineans from July to September. Littoral biocoenoses underlie a considerable regrouping every seasonal cycle due to the extreme seasonality (ZENKEVITCH 1963). "Atlantic-Boreal-temperate" terebellomorpha polychaetes penetrate far north-east in coastal and fjord areas of the Finnmark where the temperature is relative high and stable (HOLTHE 1978).

In contrast to BRATTEGARD and HOLTHE (1995, 1997) however, some other biogeographers (*e.g.* FORBES and GODWIN-AUSTEN 1859; CHRISTIANSEN 1982; HISCOCK 1998; GLÉMAREC 1998/2000/pers. comm.) described the southern boundary for many Arctic forms and a northern boundary for many southern organisms at the Lofoten islands.

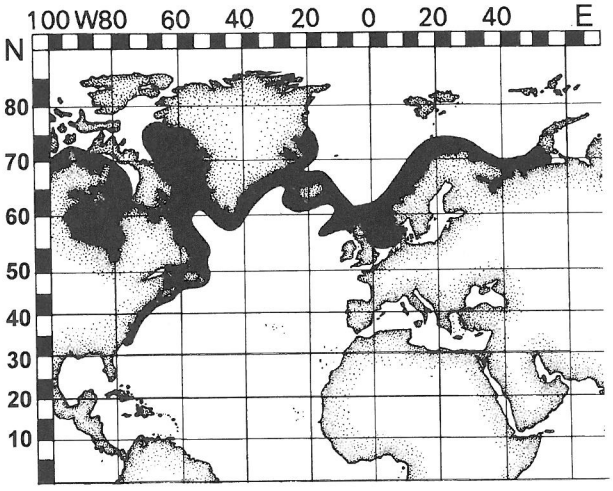


Fig. 100: *Thysanoessa raschii* as an example for a cold-water neritic range distribution pattern (from VAN DER SPOEL and HEYMAN 1983, clipped).

VAN DER SPOEL and HEYMAN (1983) classified the coastal areas from the southern Barents Sea along the Norwegian coast, the Shetland and Faeroe Isles, and Iceland to SE-Greenland with *Thysanoessa raschii* as an example for a species with a cold-water neritopelagic distribution pattern (Fig. 100). The diatom *Thalassiosira gravida* is confined to the same Subarctic neritic distribution belt in its northern hemisphere populations (SEMINA 1997).

The Greenland-Iceland-Faeroe Rise separates the deep North Atlantic Ocean from the Norwegian-Greenland Sea and therefore from deep Arctic Ocean waters (Chaps. 3.1; 3.2; 3.3). Thus, it is a distribution barrier for many taxonomic groups *e.g.* isopods (SVAVARSSON et al. 1990, 1993; NEGOESCU and SVAVARSSON 1997; SVAVARSSON 1997, 1999) and gammaridean amphipods (DAHL 1979; WEISSHAPPEL and SVAVARSSON 1996) resulting – together with a short evolutionary time – in a low diversity of the deep

Arctic faunas.

The **South Iceland-Faeroe Shelf province** is influenced by complex current patterns. A branch of the cold East Greenland Current – the East Iceland Current – submerges with its cold polar water masses along the northern slope of the Iceland-Faeroe Rise and towards the Norwegian continental slope in-between NAD water masses above and Norwegian Sea Deep Water (NSDW) below. The surface waters at the southern slope of the Iceland-Faeroe Rise are influenced by warm and more saline Atlantic waters of the NAD and the Irminger Current which is deflected towards the south-west, while cold deep waters from the Norwegian Basin intermittently overspill the Iceland-Faeroe Rise with a saddle depth of ~ 500 m between Iceland and the Faeroes and ~ 850 m at the Faeroe Bank Channel. This cold Norwegian Sea Deep Water flowing through the Faeroe Bank Channel bathes the southern flanks of the Iceland-Faeroe Rise at depths exceeding ~ 800 m. A weaker and variable eastern branch of the Irminger Current flows clockwise around NW-Iceland transporting slightly warmer and Atlantic surface waters of higher salinity to shallow near-shore areas of North Iceland (Chap. 3.3) with implications on local diversity (Stefánsson 1962, 1969; Stefánsson and Guðmundsson 1969; Westerberg 1979; Blindheim and Loeng 1981; Meincke 1983; Malmberg 1985, 1986; Blindheim 1990; Hansen et al. 1990; Malmberg and Kristmannsson 1992; Reinert 1995). Thus, biogeographic patterns are different according to depth and related to water masses, and at shallower depths also to habitat diversity (Kotthaus and Krefft 1967; Haedrich and Krefft 1978; Svavarsson et al. 1993; Weisshappel and Svavarsson 1996; Merret and Haedrich 1997).
Shallower waters show impoverished Boreal biogeographic patterns, although this province is situated already at comparatively high latitudes. Intertidal and subtidal patterns around Iceland show rather more a clockwise dropping out of species than a replacement by northern Arctic species and reflect the patterns of different substrate types and habitats instead of temperature boundaries. No endemic Arctic species were recorded at such shallow waters at Iceland (Ingólfsson 1996). There are only very few records of *Lophelia pertusa* corals to the south-east of Iceland and on the Iceland Faeroe Rise despite a high abundance on the banks south of the Faeroes (Frederiksen et al. 1992; Rogers 1994; Magnússon and Magnússon 1995) and it is not quite clear by which factor the abundance is limited in this area.

Already Forbes (1859) described the marked biological differences between the north(east) and the south and west coast of Iceland. Ekman (1953) pointed out the differences between north and south of the Greenland-Faeroe-Scotland Ridge system and Earll and Farnham (1983) indicated the absence of the typical boreal species *Alcyonium digitatum* along the northern coast. The record table of NEA cool-temperate brachyura of Christiansen (1982) discriminated also the different Icelandic shelf provinces and described differences from other adjacent Boreal-Arctic and Boreal areas as *e.g.* the Norwegian subprovinces, Shetland, and the North Sea. Magnússon and Magnússon (1995) gave a valuable characterisation of the Icelandic waters for fishes on the continental slope.
Alvarez et al. (1988) found a new floristic area comprising Iceland, the Faeroes, and Shetland islands by clustering seaweeds in relation to possibly distribution limiting factors.
Gammaridean amphipod diversity in shallow to intermediate depths was compared between the Reykjanes Ridge area south-west of Iceland and the Kolbeinsey Ridge area north of Iceland by Weisshappel and Svavarsson (1998). Temperature, rapidly declining with increasing depth, is the most important environmental variable for the differentiation of species composition and distribution in the northern area. Depth worked out to be the most important environmental variable for the southern area, explained by a shorter evolutionary time for shallow water organisms after the Pleistocene glaciations. Related to the origin and character of three different water masses there was identified a benthic zonation off the northern Icelandic coast: Shallow coastal areas bathed in slightly warmer North Atlantic Water of higher salinity, an intermediate deep (~ 250-350 m) zone adjacent to the north, which is influenced by polar water masses of the East Iceland Current with a slightly lower salinity, and further to the north a deeper zone lying in very cold Norwegian Sea Deep Water also with a lower salinity (Weisshappel and Svavarsson 1998).

The entire region is characterised furthermore by a strong seasonality, most significant in solar radiation, and cool waters with a very high productivity. Especially zooplankton biomass is indicated as being extraordinarily high (Couper 1989).

Units of cold Arctic water masses:
Marine biology occupies a dominant role in the Arctic ecosystems, and many nearshore terrestrial ecosystems depend heavily on marine biological production immediately offshore even though solar insulation is available only seasonally and often screened by snow and sea ice. (ALEXANDER 1992; BLEAKLEY and ALEXANDER 1995). The development of phytoplankton of the Arctic basin is closely bound up with ice conditions (Chap. 3.5). The mass development of the spring plankton (mainly diatoms) coincides with melting of the ice and penetration of light into the water column. There is a gradient from the seas adjacent to the Pole with less than a month (August) to the south-west of the Barents Sea with about eight months of vegetation period (ZENKEVITCH 1963).

The Arctic, with an age of ~ 3.0-3.2 mio years (to other opinions with its present appearance only 2.5-1.8 mio years [GOLIKOV et al. 1990]) and being ~20 mio years younger than the Antarctic cold water system, has had comparably fewer time to develop endemics. Consequently there are very few endemics at higher taxonomic levels (BRIGGS 1995), although there are significant numbers of endemic species. ZENKEVITCH (1963) considered more than 50% of the Arctic basin slope fauna to be endemic to the Arctic Ocean. The Arctic and Arctic-cold boreal fauna was described as descending from evolutionary centres in the Pacific despite the present hydrological situation (*e.g.* MENZIES et al. 1973; BOUCHET and WARÉN 1979; GOLIKOV et al. 1990; BRIGGS 1995). DUNTON (1992) highlighted the paradox that the Arctic fauna shows high affinities to a Pacific origin whereas the Arctic macro-flora seems to be entirely of Atlantic origin. BOUCHET and WARÉN (1979) indicated 83% endemic shell bearing Arctic deep-sea molluscs. VAN DEN HOEK (1975) gave an endemism rate of only 6% for seaweeds. According to Svavarsson et al. (1993) the endemism rate for Arctic asellote isopods on species level is < 30% at depths < 500 m, < 50% at depths < 750 m, but increases to > 60% at depths > 750 m, and up to > 90% in the deepest abysses of the Arctic Seas.
Species number is poorer but number of individuals higher in the extreme habitats of the Arctic, according to Thienemann's law. PAUL and MENZIES (1974) emphasised that this rule of oligomixity applies also to the Arctic benthos where benthic biomass is extremely low especially in the high Arctic region.

The Arctic basin is an enclosed mediterranean sea with a very limited water exchange with the world ocean. Only a minor inflow (~ 30%) takes place through the Bering Strait with a sill depths of ≤ 45 m, most of which passes into the NW-Atlantic through the Canadian Arctic West-Greenland waterways, whereas the major inflow (~ 70%) happens through submerging water at the eastern side of Fram Strait along the continental margin around Spitzbergen/Svalbard, besides freshwater runoff from (Siberian) river catchments and glacial meltwater. The only outflow from the Arctic Ocean occurs on the western side of Fram Strait which is also the only deep-water connection with depths ≥ 2600 m between the Arctic and the Norwegian-Greenland deep-sea basins (Chap. 3.3; Figs. 10, 15).

HOLTHE (1978) showed that elements with an Arctic affinity were able to survive all over the area whereas Atlantic Boreal-temperate elements failed to colonise cold, deep, or shallow highly variable basins by analysing the distribution of terebellomorpha polychaetes of the entire northern European waters from the eastern English Channel to Svalbard/Spitzbergen.

For the eastern boundary between the Cold Arctic and the Cool-temperate biogeographic provinces in the North Atlantic it was stated that it is not the same for the bottom and the pelagic fauna (*e.g.* ZENKEVITCH 1963). The pelagic boundary in the Barents Sea lies much farther to the north and east than the benthic boundary (compare Fig. 104 and Figs. 105, 106) due to considerable temperature differences between the upper water body of warmer Atlantic waters and the colder sea floor. This is contrary to the western North Atlantic region which is influenced by the cold East Greenland current and patterns are *vice versa* with a pelagic boundary shifting farther south-west towards Newfoundland.

A subdivision of the East Greenland coast into a Subarctic and (High) Arctic region by DUNBAR (1985, Chap. 5.1.22) and EKMAN (1953) corresponds well with the delimitation given in this study which separates the **North-East Greenland Shelf province** from the **South-East Greenland and North Iceland Shelf province**. Latter region is characterised by water masses of the cold East Greenland current with lower salinity with its

periodically and seasonally fluctuating ice cover, drift ice and very cold Norwegian Sea Deep Water respectively Greenland Sea Deep Water masses overflowing the sill of the Greenland-Iceland rise in Denmark Strait with a saddle depth of ~ 600 m. A branch of the cold East Greenland Current – the East Iceland Current – bathes the northern Icelandic coast with fluctuating intensity and in interference with the shallow warmer near-coast north-eastern branch of the Irminger Current. The cold polar waters of the East Iceland Current submerge along the northern slope of the Iceland-Faeroe Rise towards the Faeroes and the Norwegian continental slope into intermediate depths with intermittent overspills across the rise into the North Atlantic basin (Chap. 3.3) (AAGAARD and COACHMAN 1968; STEFÁNSSON 1962, 1969; STEFÁNSSON and GUÐMUNDSSON 1969; VINJE 1980; BLINDHEIM and LOENG 1981; MEINCKE 1983; MALMBERG 1985, 1986; BOURKE et al. 1987; BLINDHEIM 1990; MALMBERG and KRISTMANNSSON 1992;).
Temperature, rapidly declining with increasing depth, was identified to be the most important environmental variable for the differentiation of species composition and distribution in bathymetric belts, which are composed of different water masses off northern Iceland (WEISSHAPPEL and SVAVARSSON 1998). The north-eastern branch of the Irminger Current with warmer and Atlantic waters of higher salinity is phasing out in a shallow fringe near the northern Icelandic coast (INGÓLFSSON 1996). This stretch with its still slightly boreal character is part of the South Iceland-Faeroe Shelf province. Adjacent to the north there is an intermediate deep (~ 250-350 m) zone, which is influenced by polar water masses of the East Iceland Current with slightly lower salinity, and further to the north a deeper zone lying in very cold Norwegian-Greenland Sea Deep Water of also slightly lower salinity, both with different species compositions (WEISSHAPPEL and SVAVARSSON 1998). In contrast to these findings concluded BRANDT (1993) and BRAND and PIEPENBURG (1994) that differences in peracarid crustacean assemblages on a transect of the Kolbeinsey Ridge were probably due to sediment composition and and food supply rather than to hydrographic conditions.

A (not yet clustered) analysis of the distribution of benthic macro-organisms comparing Jan Mayen, Svalbard (Spitzbergen), and Bear Island (GULLIKSEN et al. 1999) gave evidence for biogeographical differences between Jan Mayen and the other areas and justifies an incorporation of Jan Mayen in the South-East Greenland – North Iceland Shelf province. Such species with a different distribution were *e.g.* the crustaceans *Balanus balanus, Hyas araneus, Hyas coarctus*, the sea anemone *Hormathia nodosa*, the ascidians *Boltenia echinata, Halocynthia pyriformis, Styela rustica*, and the echinoderm *Ctenodiscus crisatus* which were absent at Jan Mayen but common at Svalbard/Spitzbergen (GULLIKSEN et al. 1999). *Hyas araneus* and *H. coarctus* were described for North and East Iceland on the other hand (CHRISTIANSEN 1982).

VAN DER SPOEL and HEYMAN (1983) presented a distribution map of the neritic species *Pontegenia inermis*, which is endemic to the Subarctic regions, on the western side of the Atlantic and thus only distributed along the South-East Greenland coast but not at the eastern Subarctic coasts in the OSPAR area. Further evidence for a separate South-East Greenland – North Iceland Shelf province was given by ALVAREZ et al. (1988). They revealed in their statistical analysis of relationships between seaweeds and possibly distribution limiting factors that the southern Greenland seaweed flora appeared to be segregated from those floras of Arctic Canada and Spitzbergen/Svalbard.
The "Times Atlas and Encyclopaedia of the Sea" (COUPER 1989) shows the world's highest benthic biomass and PIERROT-BULTS (1997) also a very high phytoplankton productivity in the area of the South-East Greenland and North Iceland Shelf province.

There is a subdivision in the permanently pack ice-covered high Arctic between the deep-water **High Arctic Maritime province** and a shallower **North-East Greenland Shelf province** due to differences in species composition, abundance, and productivity related *i.a.* to pelagic-benthic coupling as described in chapter 3.5.
The higher and more clearly pronounced diversity of the Greenland Sea pelagos compared to the one of the Arctic Basin (VINOGRADOV 1968) gives further evidence for a combination of pelagic and ice-cover related classification characteristics to segregate the "impoverished" High Arctic Maritime province.
Also ZEZINA and VINOGRADOVA (1998) gave delimitations between high Arctic deep water, Barents Sea, North-East Greenland, and South-East Greenland shelves for the benthic realm that correlate with the classification given in this study.

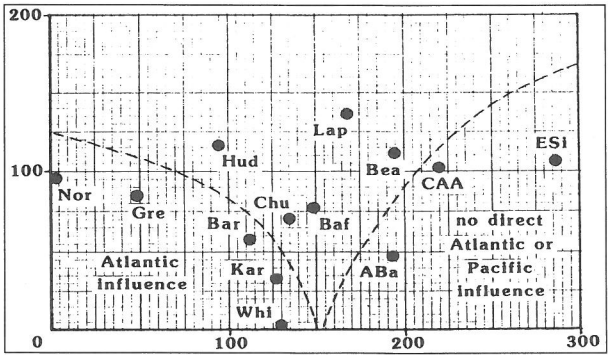
Due to remoteness and inaccessibility of the ice-covered region, marine biological research on the North-East Greenland Shelf had not produced much information on biogeographical data in the past, but had dominantly focussed on the feature of the Northeast Water Polynya (NEWP) in the last decade (Chap. 3.5.1). EKMAN (1953) considered the North-East Greenland waters being of high Arctic character north of 68°N in contrast to a low Arctic region to the south-east of Greenland. CHRISTIANSEN (1982) indicated the absence of brachyura crabs as a characteristic for NE-Greenland. Southerly species with long larval stadiums cannot drift against the cold East Greenland Current and larvae do not have sufficient time to complete their development with a plankton bloom lasting only 1-1.5 months, besides surface waters being too brackish for many larvae to survive.

The **Barents Sea province** is influenced by an ice cover, shifting seasonally over a wide range, and different water masses which give this province its fluctuating, heterogeneous, and seasonally influenced character: warm and saline descendants of the NAD and cold Arctic water masses and currents of lower salinity besides freshwater influence and ice-edge dynamics. Dense warmer and modified Atlantic water of higher salinity intrudes the deeper part of the Barents Sea below the brackish surface layer and transformed bottom water which increases towards the eastern part. More brackish and warmer water masses of the coastal current characterise the Finnmark subprovince to the south. The Arctic Front is more clearly pronounced in the western part, but more diffuse in the eastern part where there is extensive mixing between Atlantic waters and Arctic water masses of the Persey Current and formation of Arctic Deep Water takes place (Chap. 3.3; Fig. 15). There are seasonal, short-term, and long-term variations in ice conditions in the Barents Sea with a decrease of 40% of the permanent ice covered area during the last 23 years. The maximum seasonal extension however did not show a significant decline in the same period (BLINDHEIM and LOENG 1981; VINJE 1980, 1985; SKJOLDAL and REY 1989; LOENG 1991; VINJE and KVAMBEKK 1991). These highly dynamic situation finds its expression in pelagic as well as in benthic biological patterns (*e.g.* ZENKEVITCH 1963; REY and LOENG 1985; HASSEL 1986; DRAGESUND and GJØSÆTER 1988; MEHLUM 1989, 1990; LØNNE and GULLIKSEN 1991a, b; SAKSHAUG et al. 1994; HANSEN et al. 1996; GJØSÆTER 1994, 1997; GJØSÆTER and USHAKOV 1997; MEHLUM et al. 1998).
More than 20% of the Barents Sea shelf is shallower than 100 m but there are several troughs deeper than 400 m and the shelf-break is comparatively deep in wide parts, reaching down to 400-600 m before the shelf "breaks" into the Norwegian and Arctic basins (Fig. 10) (GJØSÆTER 1997). There are different boundaries between the Arctic and the Atlantic boreal faunas for the pelagial and the benthal in the Barents Sea as mentioned above (compare Fig. 104 and Figs. 105, 106) (*e.g.* ZENKEVITCH 1963; DRAGESUND and GJØSÆTER 1988). The fauna impoverishes towards the north and the east in the Barents Sea, due to a decreasing influence of warm saline Atlantic waters.
Phytoplankton production seems to be more related to seasonal changing light conditions and water stratification then to the retreat of the ice-edge (REY and LOENG 1985). However, the shifting Arctic Front (Chap. 3.3, Fig. 15) as well as sea ice in its varying extension and structure has important effects on phytoplankton and the following food web as described in chapter 3.5. The different and changing structures of the ice margins in the Barents Sea with leads and ice edges result in a diversified distribution and foraging behaviour of marine birds (MEHLUM 1989, 1990; HUNT et al. 1996; MEHLUM et al. 1998).
Fish species can be classified into Arctic, Arctic-Boreal, and Boreal zoogeographic groups related to the hydrographic gradient in the Barents Sea (EKMAN 1953; DRAGESUND and GJØSÆTER 1988). The capelin (*Mallotus villosus*) plays a major role in the Barents Sea ecosystem *i.a.* as a nutrition base for seals, whales, and birds (*e.g.* ANKER-NILSSEN et al. 1996; HANSEN et al. 1996; GJØSÆTER 1997; MEHLUM et al. 1998).

Disappearance of boreal and Subarctic forms, being replaced by high Arctic species, result in patchy patterns of benthic biota and distribution of benthic biomass. A gradient of impoverishment of the qualitative composition of benthos and plankton can be observed along the Murman coast towards the north-eastern parts of the Barents Sea and beyond Novaya Zemlya. Latter islands are a distinct biogeographical boundary (ZENKEVITCH 1963). Especially the fauna and flora of the upper layers are particularly affected by the saline gradient and brackish layering, caused by melting processes and terrestrial runoff, and the influence of long and extreme ice conditions. Some littoral populations have vanished in northern and eastern parts of the Barents Sea due to coastal ice. The shallows in the south-eastern and central Barents Sea and the southern and

eastern slopes of Spitzbergen show the richest benthos in species numbers whereas the south-western half of the Barents Sea has quantitatively the richest plankton.
The border between the Atlantic-Boreal and Arctic biogeographical regions lies at depths of 30-40 m in the White Sea, and eastern parts of the Barents Sea according to GOLIKOV et al. (1990). A more differentiated map of zoogeographical subdivisions, reflecting the complicated situation of the Barents Sea, was given by ZENKEVITCH (1963, p. 175). Benthic biomass in the Barents Sea is extraordinary high (ZENKEVITCH 1963; COUPER 1989). Richness in pelagic and bottom life is ensured by strong vertical circulations and saline input. For the Barents Sea, providing one of the highest fishery yields, it is remarkable that nearly all main commercial fish (cod, haddock, bass, coalfish, capelin, and herring, excluding Arctic cod) are at extreme limits of their distribution and feed only in the Barents Sea but they breed mainly outside the Barents Sea in the coastal waters of Norway (ZENKEVITCH 1963; DRAGESUND and GJØSÆTER 1988; GJØSÆTER 1994; HANSEN et al. 1996). The temporal meso-scale physio-oceanographic variability of the Barents Se ecosystem has great implications on production, abundance and species distribution (BLACKER 1957; LOENG 1987; MIDTTUN and LOENG 1987; SKJOLDAL and REY 1989; BLINDHEIM and SKJOLDAL 1993; ANKER-NILSSEN 1996).
The Barents and White Seas show warm- and cold-water relicts as characteristic features resulting from climatic alternations in the Quaternary period encountered frequently in small scale habitat areas (ZENKEVITCH 1963).

The **White Sea** should be regarded as a **subprovince** of the Barents Sea depending on the scale of the biogeographical hierarchy used. Evidence for such a subdivision of the semi-closed epicontinental White Sea was given generally by DUNBAR (1951, 1953), GOLIKOV et al. (1990), and especially by ZENKEVITCH (1963).
The White Sea, with a maximum depth of 330 m, was indicated to have a distinct boreal and much more seasonal and brackish (summery stratified in surface 4-10 ‰ and depths 21-34 ‰ layers) character compared to the Barents Sea and is furthermore influenced by a high tidal range (< 8.5 m) with strong tidal currents in the Gorlo-channel. Below the fresher surface layer there is a strong salinity gradient between the western and the eastern coast of the Gorlo-channel connecting the White and the Barents Sea due to the influx of the NAD-North Cape current descendant, also expressed in the abundance of related biota. Ice-cover lasts for more than half of the year, with landfast ice and ice-floes even remaining longer, but there are warmer summers of continental climate type in contrast to the south-western Barents Sea area. EKMAN (1935, 1953) regarded the White Sea as an isolated high Arctic relict region and presented distribution maps of the post-glacial relic *Portlandia arctica* in the White Sea isolated from the Barents Sea, whereas *Pandalus borealis* was shown to be present in the Barents Sea but absent in the White Sea.
Also LONGHURST (1998) gave the White Sea a character different from the Barents Sea (Boreal Polar province versus Atlantic Subarctic province) in his classification.
RIDGWAY and HARRISON (1981b, 1985) and HANSEN et al. (1996) presented distribution maps and descriptions of *Phoca hispida* (ringed seal) that excludes the White Sea despite its rather similar character to the northern and eastern Baltic Sea where this marine mammal species occurs. Also *Halichoerus grypus* (grey seal), *Phoca vitulina* (harbour seal), *Erignathus barbatus* (bearded seal), *Balaenoptera acutorostrata* (mink whale), and *Lagenorhynchus albirostris* (white-beaked dolphin) live in (parts of) the Barents Sea but does not seem to enter the White Sea according to descriptions of these authors. The majority of the *Phoca groenlandica* (harp seal) population that feeds in the Barents Sea in summer breeds on the White Sea ice (BENJAMINSEN 1979; DRAGESUND and GJØSÆTER 1988).
There are very few endemics in the White Sea but a certain number of warm- and cold-water relics and a flora and fauna of very impoverished Barents Sea character, due to the harsh climatic conditions. The White Sea is the western distribution limit of a series of Pacific Ocean forms and shows similarities with the Baltic Sea, resulting from post-glacial connections, at the same time. There is a vertical differentiation with predominating high Arctic pseudo-abyssal animal forms at depths, low Arctic forms characteristic for the upper 30-40 m, north-boreal communities in the littoral zone, and thermophilic and oligohalophilic forms in the summery surface layer (ZENKEVITCH 1963; GOLIKOV et al. 1990). The White Sea neritic waters have been classified as a region of its own but with relations to the Barents Sea by OKOLODKOV and DODGE (1996) on the base of planktonic dinoflagellates (Figs. 101, 102). Those planktonic dinoflagellates of boreal origin which penetrate from the White Sea into the Barents Sea were regarded as allochtonous immigrants.



ABa - Arctic Basin; Bar - Barents Sea; Baf - Baffin Bay; Bea - Beaufort Sea; CAA - Canadian Arctic Archipelago; Chu - Chukchi Sea; ESi - East Siberian Sea; Gre - Greenland Sea; Hud - Hudson Bay; Kar - Kara Sea; Lap - Laptev Sea; Nor - Norwegian Sea; Whi - White Sea

Fig. 101: Ordination diagram of the Arctic region relationships, based on the DECORANA analysis of planktonic dinoflagellates (from OKOLODKOV and DODGE 1996).

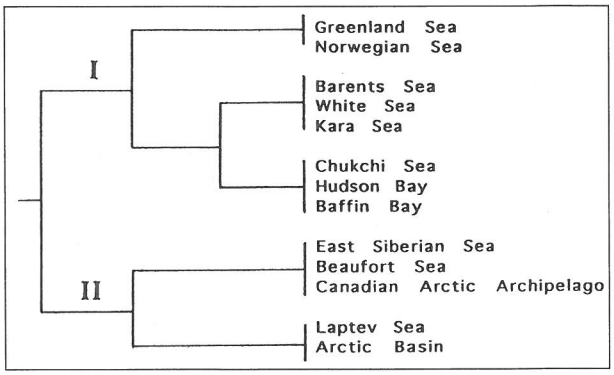


Fig. 102: Cluster diagram of the Arctic region relationships, based on the TWINSPAN analysis of planktonic dinoflagellates (from OKOLODKOV and DODGE 1996).

6.3.3 Deep-Sea

The abyssal of the world ocean is characterised by rather monotonous environmental conditions without sharp gradients including low temperatures (*e.g.* < 0°C in the North Polar and Norwegian-Greenland basins and ~ 2°-8° C in the NEA and NWA basins; except at hydrothermal vents), absence of light, high hydrostatic pressure increasing with depth, mainly soft muddy bottom substrates, and extremely limited food resources. While annual/seasonal fluctuations in temperature stop at about 200 m depth (EKMAN 1953) there are even major seasonal pulses and inter-annual variations in the vertical flux of particulate organic matter to large areas of the deep-sea (*e.g.* TYLER 1988; THIEL et al. 1989; RICE et al. 1994; SCOR 1994).
Besides a differentiation in central ocean and ocean margin localities, the benthos is confined to soft sediments, rare hard substrates, and more "oasis"-like communities of hydrothermal vents and cold/hydrocarbon seeps. On a global scale there is a logarithmic decrease in biomass with increasing depth and less clearly in latitudinal patterns (SCOR 1994).

Until only two decades ago the deep-sea was believed to be relatively poor in species and to be globally quite homogeneous in species distribution and abundance but the last decades have revealed a quite high diversity of biota that live on the vast muddy bathyal slopes and abyssal plains. These uniform deep-sea conditions led earlier deep-sea scientists as *e.g.* participants of the Danish Galathea expedition (*e.g.* KIRKEGAARD 1954; BRUUN 1956, 1957; MADSEN 1961; WOLFF et al. 1961; HANSEN 1967; KNUDSEN 1970) to the assumption of deep-sea species being mainly cosmopolitans. Representatives of all major classes of marine invertebrates and fish got adapted to such environments (VINOGRADOVA 1997). Even in these remote depths a single square meter may contain up to 250 species of macro- and meiobenthic invertebrates (SMITH et al. 1998). Deep-sea sediments have been estimated to harbour between 500,000 and maybe exceeding 10 million species of macrobenthos with the former number being considered low (GRASSLE and MACIOLEK 1992; SMITH et al. 1998). Locally there might be a high diversity of biological distribution patterns on spatial scales from millimetres to kilometres due to variations in food input as *e.g.* seasonal phytodetritus pulses from surface blooms or carcass falls, biogenic disturbance as *e.g.* bioturbation or megafaunal predation, or environmental heterogeneity caused by physical features as *e.g.* benthic storms, substrate differences or different water masses, etc. (GRASSLE 1989, 1991; REX et al. 1997). GAGE and TYLER (1991) and GAGE (1997) considered different types and strengths of currents in the deep-sea (Chap. 3.3) to contribute to habitat heterogeneity and thus deep-sea biodiversity on ≥ kilometre scale. DAYTON and HESSLER (1972) emphasised biological disturbance

to be an important factor for maintaining diversity in the deep-sea. JUMARS (1976) stressed the circumstance that biocoenotic compositions and distribution patterns might differ considerably within short distances and between different taxa. As in surface ecosystems it seems likely that an integration of both ecological and evolutionary processes contribute to shaping patterns of biodiversity in the deep-sea and that their effects depend on spatial and temporal scales (REX et al. 1997). Thus, macrobenthic species richness in the deep-sea can be substantially greater than in shallow waters (GAGE and TYLER 1991; GRASSLE 1991; GAGE 1996, 1997).
But there are also a number of deep-sea settings where species richness is low and dominance is high due to Thienemann's law concerning extreme environments. According to GRASSLE (1989) and LEVIN and GAGE (1998) such environments include oxygen minimum zones beneath upwelling regions, isolated basins, hydrothermal vents, or aspects of seamount biota (ZEZINA 1997).

There exist(ed) three main views about deep-sea marine zoogeography, as VINOGRADOVA (1997) set out:
- Species distributions are global or at least extremely wide ranging due to the absence of ecological barriers in a widely homogeneous deep-sea;
- Deep-sea communities are limited by topographic and meso-scale water mass features in multiple basins;
- Deep-sea species are related to ~ 4 ocean divisions with several hierarchical subdivisions according to the taxonomic level;

At this point, again the question of modern genetically based species definitions has to be taken into account. Assumed wide distribution ranges of morphologically determined deep-sea species might change if they turn out to be composed of several different species (compare Chap. 5).

REX et al. (1993) stated a "latitudinal species-diversity gradient" (LSDG) for small benthic deep-sea invertebrates or REX et al. (1997) more generally described a decreasing diversity related to latitudinally changing environmental factors from equatorial/tropical latitudes to the poles. This is similar to the decline in species diversity in the pelagial, the shallow coastal seas, or of terrestrial flora and fauna. GAGE and MAY (1993) on the other hand stressed the vertical gradient of diversity increase with increasing depth and compared it with the gradient when one descends from mountain tops to sea level.

The geographical extent of species' ranges is related to the amplitude of vertical distribution and increases with depth or in other words the greater the eurybathy of a species the wider its geographical range and the more the distinctness of deep-sea faunas the deeper the environment (REX 1981, 1983; VINOGRADOV 1997; VINOGRADOVA 1997; ZEZINA 1997).
The large scale distribution of deep-sea organisms is mostly related to temperature as determining environmental factor similar to shallow water patterns. However LEVIN and GAGE (1998) tried to reveal other factors as oxygen, depth, sediment organic carbon content, particle size, latitude that could be responsible for species diversity control, but did not find a master variable. These factors might show higher significance on smaller scales of deep-sea species distribution. GEORGE (1979) considered pressure to be an important environmental factor in the deep-sea which created three different adaptive strategies: pressure-sensitive species that might immigrate to moderate depths only with physiological stress, metabolically insensitive deep-sea colonisers, and species being only capable to adapt to moderate pressure ranges. Availability of food is an other determining factor for deep-sea distribution patterns. Presumably less than 3% of the surface primary production reaches the abyssal depths > 3000 m (THIEL et al. 1989; SOKOLOVA 1997). With increasing depth food becomes increasingly scarce what has its reflections in feeding patterns. Below 3000 m the energetic costs for active forage become too high. Thus feeding patterns of carnivores change from being active to a more ambush type, as well reflected by their morphology and physiology (THIEL et al. 1996; VINOGRADOV 1997).

Spatial heterogeneity in the deep-sea varies with time as concerning the seasonally varying pulse of organic carbon flux from the surface of both temperate and subtropical latitudes and physical variability with current variations from semi-diurnal tides to seasonally changing abyssal currents (TYLER 1988, 1996). Besides polar regions, where both highest and lowest flux levels have been recorded, there is a linear relationship between vertical organic carbon flux and surface primary production (LAMPITT and ANTIA 1977). Vertical

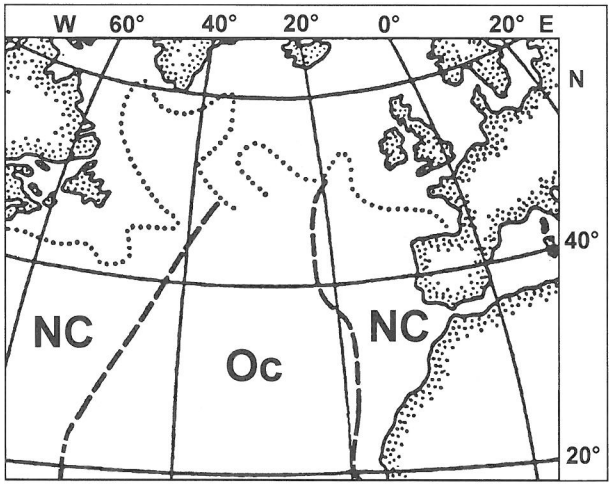
nutrient flux can be unpredictable as *e.g.* fall of large carcasses or aggregations of macrophytes, or seasonally predictable as *e.g.* rain of POM with peaks in the northern NEA in July which might have implications on reproductive cycles of deep-sea organisms (TYLER 1988).
The abyssal plains below the centres of the subtropical gyres are generally regarded as being food-limited oligotrophic areas, or sometimes called abyssal deserts, induced by low surface production (GAGE and TYLER 1991; ROWE 1996).
There have been made several comparisons between seasonally influenced stations at the Porcupine Seabight Abyssal Plain (PAP) and subtropical oligotrophic stations mainly at the Madeira Abyssal Plain (MAP) regarding phytodetritus deposition, consumption by nano-, meio-, and macrofauna and probably related megafaunal patterns (*e.g.* IOSDL Deepseas Programme) (*e.g.* THIEL 1983; THIEL et al. 1989; RICE et al. 1994). THIEL et al. (1989) estimated 0.3-3% of the spring surface primary production to sediment to the deep-sea floor in the centre of the West European basin which lies in-between the higher productive European shelf-break frontal areas and the subtropical oligotrophic mid-ocean areas. It was assumed that sinking duration is 4-8 weeks from euphotic surface waters to 4500 m depth. Detrital material could be classified into the categories snow, aggregates, flocs/flakes, and particulate matter. Such particle size differences might be related to deep-sea species diversity as emphasised by ETTER and GRASSLE (1992). The fresh phytodetritus was colonised by benthic foraminifers, nematodes, harpacticoids and kinorhyncha copepods as well as holothurians, amphipods, and actinians feeding on this food source. Seasonal phytoplankton particel flux that produces a patchy detrital layer in the Porcupine Seabight was documented by BILLET et al. (1983). Accumulation was observed from April to July in depths between 1370 and 4100 m with an assumed sinking rate of 2000 m in 2-3 weeks. It was considered whether this seasonality is responded by reproductive cycles of deep-sea echinoderms.
Nematode abundance, biomass, and vertical distribution was significantly related to different phytodetritus deposition patterns of the PAP and oligotrophic stations (LAMBSHEAD et al. 1995; VANREUSEL et al. 1995).
MERRETT (1987) argued whether a considerable vertical and horizontal variation in the pelagic and benthic standing crop which is related to differences in seasonal surface production is responded by different assemblages of abyssal demersal fish species. He described a marked faunal change between areas of permanently stratified waters to the south and winterly mixed waters to the north of a boundary at ~ 40°N in the eastern North Atlantic. Southern assemblages consisted mostly of negatively benthic to close neutraly buoyanced benthopelagic microphagous feeding small species whereas northern communities were predominated by large swimbladdered benthopelagic macrophagous rattails.
Similar differences between a northerly station with dominating necrophagous fish in the northern PAP and two southerly stations with markedly dominance of scavenging decapods (*Plesiopenaeus armatus*) on the subtropical MAP have been described by THURSTON et al. (1995) or regarding abundance, biomass, structure of abyssal invertebrate megafauna by THURSTON et al. (1994, 1998). Later works emphasised the presence of particle-selective phytodetrivorous holothurians on the Porcupine Seabight Abyssal Plain.

Organic matter in the sediment and in suspension close to the bottom (benthic boundary layer/BBL) is the main food source for most benthic deep-sea invertebrates. The suprabenthic pelagic zone seems to be inhabited by a distinct community of nektonic and planktonic species quite different to that living at comparable depth in abyssopelagic zones above the BBL (ANGEL and BAKER 1982; ELLIS 1985).

According to SOKOLOVA (1997) deposit-feeders (benthophages) predominate in eutrophic regions below high surface production, while in oligotrophic regions, where sedimentation rates are low and organic matter is rare, suspension-feeders (sestonophages; triptono-, detritus-, and zoophages) predominate but in a very low population density. Besides this two basic types there are carnivores (predators and scavengers) in the deep-sea. Conditions are generally more eutrophic in the deep Atlantic compared with other oceans (SOKOLOVA 1997) and especially in the abyssal of the south-western oceanic OSPAR area with decreasing trophical status towards the south (compare Figs. 96-99). SOKOLOVA (1997) delimited the central oceanic eutrophic area of the North Atlantic against the near-continental eutrophic hemipelagic sediment section at ~ 20°W and across the Newfoundland Basin on the western side of the OSPAR area (Fig. 103).
SOKOLOVA (1997) distinguished three main types of species distribution due to feeding habits: near-continental, oceanic, and panthalassic (for species which penetrate from eutrophic into oligotrophic areas).
According to this differentiation there has been reported a predominance of deposit-feeders in the Norwegian

Basin, the Iberian Basin and the Bay of Biscay (SOUTHWARD and SOUTHWARD 1967; THIEL 1972; LAUBIER and SIBUET 1977; GRASSHOFF 1985; SIBUET 1977, 1979, 1985; SOKOLOVA 1997) and primarily holothurians universally throughout the North Atlantic with a changing ratio concerning suspension-feeder predominance towards the oligotrophic central Atlantic Ocean (SOKOLOVA 1997).

Others as *e.g.* HESSLER and JUMARS (1974) and PATERSON et al. (1998) rejected SOKOLOVA's theory and furthermore could not find particularly abyssal trophic groupings, diversity and community structures directly related to production. However these authors used polychaetes for their analyses, an organism group that had proven already in relation to other questions (compare Chap. 6.1) to show a distribution behaviour different from other deep-sea organisms.



NC: Near Continental Eutrophic
Oc: Oceanic Eutrophic

Fig. 103: Trophic areas of the North Atlantic deep-sea (from SOKOLOVA 1997, modified).

Differences between the physical characteristics of the water masses deeper than 2000 m are very small, almost negligible, and hence the most important biogeographical differences are regarded by most scientists as lying in differences of food supply (BRIGGS 1995; VINOGRADOVA 1997; ZEZINA 1997; LONGHURST 1998) besides a differentiation between deep moderate cold Atlantic and very cold Arctic waters within the deep OSPAR area. But on the other hand the descriptions of ZEZINA (1997) might be also interpreted in that way that bathyal distribution patterns still underlie much more thermal influences than abyssal patterns.

MENZIES et al. (1973) and VINOGRADOVA (1979, 1997) regarded topographical features of the deep-sea bottom as *e.g.* mid-ocean ridges as possible distribution barriers for abyssal organisms. This view had been criticised by MONNIOT (1979) who could not regard the MAR to be a zoogeographical barrier for tunicates. She accentuated the MAR to be rather a boundary zone of convergence where the faunas of different basins (*e.g.* around the Azores triple junction) are superposed and furthermore that the geological age and processes of the basin development has great relevance for North Atlantic deep-sea zoogeography.

THURSTON (1990) found little evidence for a segregation of different deep-sea entities in analysing necrophagous amphipod distributions between 8°-50°N in the Atlantic Ocean at abyssopelagic depths between 3144-5940 m. He regarded this species group as being panoceanic with a wide bathymetric range.

SOUTHWARD and SOUTHWARD (1967) and SOUTHWARD (1979) identified different abyssal pogonophore species compositions in the western and eastern basin of the North Atlantic separated by the MAR. GRASSHOFF (1985) considered 75% of the gorgonarians, pennatularians, and antipatharians found in the Bay of Biscay at bathyal depth to be endemic to the Atlantic, with ~ 40% to be confined only to temperate latitudes of the deep NEA and abyssal species of these groups to have mainly a wider distribution range.

CLARKE (1962), with data of molluscs, compared *i.a.* the Labrador with the Norwegian, the Newfoundland with the Westeuropean-Iberian, and the North American with the Canaries basins and gave evidence for a differentiation between a western and eastern deep-sea province in the North Atlantic. He presumed deep-sea fauna of distinct basins to be related to adjacent contiguous shallow water faunas. HAEDRICH and MERRET (1988) and MERRET and HAEDRICH (1997), on the other hand, found strong similarities between demersal fish in archibenthal and bathyal zones of the Norwegian Basin, off Iceland, and in the Rockall Trough.
Vingradova (*e.g.* 1956, 1959, 1979; 1997) (Chap. 5.1.26) differentiated three provinces in the North Atlantic with an Arctic (comprising the Norwegian-Greenland basin) subregion without giving clear evidence for her subdivisions concerning the North Atlantic at the area covered by the OSPAR convention. A synthesis of the classifications of Zezina (1997) for the bathyal (200-3000 m) and of Vinogradova (*e.g.* 1979) for the abyssal

and hadal zones (> 3000 m) was given in a zoogeographical world map of the benthos (VINOGRADOVA and ZEZINA 1998) (Chap. 5.1.27).

The deep Arctic and Greenland-Norwegian basins are filled with very cold Arctic waters of < 0° to -1.9° C which overflows the Greenland-Iceland-Faeroe-Scotland Rise at certain localities and in irregular quantities (*e.g.* WESTERBERG 1979; SWIFT et al. 1980; MEINCKE 1983; SWIFT et al. 1983; MALMBERG 1985, 1986; BEARMAN 1989; BLINDHEIM 1990; MALMBERG and KRISTMANNSSON 1992) (Chap. 3.3). With regard to the distribution of water masses with Antarctic deep water reaching far north in the northern hemisphere and into the North Atlantic basins, overlain by Labrador and Mediterranean intermediate waters (Chap. 3.3) and uniformly cold temperatures with 2-8° C in the Atlantic, the Greenland-Iceland-Faeroe-Rise depicts a markedly biogeographic barrier (*e.g.* EKMAN 1953; DAHL 1979; SVAVARSSON et al. 1990, 1993; WEISSHAPPEL and SVAVARSSON 1996; NEGOESCU and SVAVARSSON 1997) even if there are mutual relationships between the deep-sea faunas of the North Atlantic and the Arctic (BOUCHET and WARÉN 1979; SVAVARSSON 1987; SVAVARSSON et al. 1993; VINOGRADOVA and ZEZINA 1998). ZENKEVITCH (1963) indicated species of the genus *Themisto* to be key species for the differentiation between Arctic and Atlantic abyssal forms on either side of the topographical barrier. SVAVARSSON et al. (1993) segregated asellote isopods of different taxonomic levels according to Boreal or Arctic affiliations and described different horizontal and vertical distribution patterns north and south of the Greenland-Iceland-Faeroe Rise.

The formation of a saline and cold Arctic water mass corresponded with the emergence of related pseudo-abyssal Arctic genera and species and took place during the partial isolation of the Arctic from the Atlantic in the early Pleistocene, ~ 1.8 mio years ago, according to GOLIKOV et al. (1990). BOUCHET and WARÉN (1979) presumed the Arctic mollusc fauna to be largely reminiscences of the former old Pacific fauna before the formation of the Bering Strait and highlighted the zoogeographic homogeneity of the deep Arctic and Norwegian-Greenland seas.

There has been frequently stated a poverty in Arctic deep-sea endemics and/or diversity which was mainly explained by the relative young age of the deep northern seas and long geological/hydrological isolation or additionally by special ecological conditions (*e.g.* DAHL 1972; DAHL et al. 1976; BOUCHET and WARÉN 1979; SIBUET 1979; SVAVARSSON 1987; GRASSLE 1989; SVAVARSSON et al. 1990, 1993).

MERRET (1987) and MERRET and HAEDRICH (1997) pointed out differences between abyssal (4090-5440 m depth) demersal fish assemblages in the eastern North Atlantic basin that might be linked to overlying production regimes. Later authors described a northern abyssal group north of ~ 45°(41°)N, a southern abyssal group south of 22°N, and intermediate groups in-between.

SVAVARSSON et al. (1993) discussed the relatively low endemism rates of Arctic deep-sea organisms on higher taxonomic levels *i.a.* as possibly resulting from low oxygenated abyssal depths during some epochs of the Tertiary. However, later authors indicated a recent endemism rate for Arctic asellote isopods on species level being > 60% at depths exceeding 750 m which is below the Iceland-Faeroe Rise saddle depths, and up to >90% in the deepest abysses of the Arctic Seas, whereas only one single endemic asellote isopod genus was known from these northern deep-seas. Most Arctic deep-sea asellote isopod genera and species were considered to have their distribution centre in the North Atlantic from where they have originated with a predominance of eurybathic species ranges (SVAVARSSON 1987; SVAVARSSON et al. 1993).
DAHL (1979) described a high rate of gammaridean (amphipodean) species endemism of the Norwegian abyssal plain (~ 2500-3700 m) and a low affinity to the adjacent North Atlantic abyssal areas but emphasised the high affinity to Arctic and high boreal North Atlantic faunas on shallow shelves and upper continental slopes.
SIBUET (1979) differentiated *i.a.* the European, Norwegian, Greenland, and Labrador basins in analysing asteroid similarities at depths of 1800-3000 m and 3000-5000 m. Differences, but also a high degree of similarity were found between the Greenland and Norwegian basins, however the European and Labrador basins were quite dissimilar to the former and showed higher similarity only at depths of 3000-5000 m. She concluded with a confirmation of the isolating effect of topographical barriers or ecological conditions to

biogeography in deep-sea basins. In a later publication she documented also differences in holothurian and asteroid abundance that were much higher in the Greenland, Lofoten, and Norwegian basins compared to the Porcupine and Bay of Biscay basins, whereas ophiuroids were nearly absent in former basins (SIBUET 1985). VINOGRADOVA (1997) argued that the Arctic deep-sea fauna might have been formed by repeated descents of the shelf fauna under the influence of temperature and salinity oscillations resulting in a splitting off deep-sea sibling species and regarded the Arctic basin to be populated by a pseudo-abyssal fauna of deep-sea fishes, sponges, bivalves, and echinoderms. Similar were findings of KUSSAKIN (1973) or of JUST (1980a) who distinguished amphipods of the North Polar Sea to belong mainly to genera of the adjacent shelves from the sublittoral to bathyal slopes, whereas asellote isopods were identified to belong mainly to widespread deep-sea genera. Also HESSLER et al. (1979) regarded deep-water isopod families to have evolved in deep waters. HAEDRICH and KREFFT (1978) presumed recent Arctic deep-sea fishes to be secondary invaders from shallower depths and did not find fishes that evolved or radiated primarily in deep Greenland Sea Waters.

MADSEN (1961) considered the upward vertical emergence of deep-sea species in the high Arctic to be not only facilitated by similar cold temperature conditions but probably also by the absence of light throughout most of the year and the darkness in the water column resulting from the polar night, ice cover, and the low angle of radiation income.

According to GOLIKOV et al. (1990) the bathyal appears to harbour the most ancient representatives of the present-day fauna from the historical and genetical point of view, a paradigm that needs further analysis.

ZEZINA (1997) regarded mid-oceanic parts of the bathyal zone to possess very important biological characteristics with many endemic species. One major difference is that species which are living on the main continental slopes are absent in the bathyal of oceanic islands or the bathyal of mid-oceanic features. These mid-oceanic regions are usually poorer in species diversity compared to the near-continental parts of the bathyal zone, *e.g.* for the Pacific was given a ratio of 18/82%, whereas it was suggested that these regions depict marginal distribution areas or even areas of expatriation of many bathyal species usually living on slopes. These communities appear to be oligo-mixed (low divers) but with comparably numerous specimens of few species which makes this communities attractive for fishery exploitation (ZEZINA 1997).

Seamounts might be exceptional deep-sea features to these considerations and might show considerably higher biodiversity (BOEHLERT and GENIN 1987; WILSON and KAUFMANN 1987; ROGERS 1994; ZEZINA 1997) as far as not being already destroyed by fishery activities (ROGERS 1994; KOSLOW and GOWLETT-HOLMES 1998; KOSLOW et al. 1999).
Seamounts have been defined as undersea mountains which rise steeply from the sea bottom to below sealevel with an elevation > 1000 m and a limited extent across the summit. They can be further classified by their elevation heights, shape, and summit depth (ROGERS 1994). There are close similarities of biotic patterns of seamounts with those of emerged oceanic islands as has been shown between the Great Meteor Seamount and the Canary Islands and Madeira (WILSON and KAUFMANN 1987). Formation and locations of seamounts within the OSPAR area are described in the chapter 3.1.
Depending on morphological shape, latitude, stratification, and location within currents there might be complex thermohaline and flow patterns around seamounts on different scales from local to oceanic. The hydrological features associated might comprise *i.a.* internal wave reflection, local upwelling, tidal amplification, meso-scale geopotential height perturbations, deflection and modification of the incident flow, trapped thermohaline fronts, and closed circulation patterns by eddy trapping so-called Taylor columns (RODEN 1987).
Steep seamount slopes swept by accelerated currents can provide a hard substrate habitat diversity in extensive areas in otherwise soft sedimentary environments. These different hydrographical as well as morphological aspects have important effects on pelagic and benthic ecosystems above and on seamounts. For some marine biota they may be considered as islands separated by deep ocean areas. However, biological communities at seamounts may differ qualitatively and quantitatively from continental shelf and slope counterparts at similar water depths (BOEHLERT and GENIN 1987).
Different ways of recruitment of species to seamounts by different patterns of larval behaviour and flow patterns were considered by BOEHLERT and MUNDY (1993) and ROGERS (1994). Above some seamount summits

there were recorded enhanced concentrations of plankton throughout the water column, concentrated by different mechanisms, which trigger the abundance of taxa of higher trophic levels, and often result in an intensive exploitation of commercial interesting fishes (Boehlert and Genin 1987; Rogers 1994; Zezina 1997; Koslow and Gowlett-Holmes 1998; Koslow et al. 1999). Benthic biological patterns of seamounts in the NEA are still not fully understood and due to the nearly complete destruction of the original benthic status of many seamounts by deep fisheries there is no possibility anymore to get a baseline of original biocoenoses for a future monitoring or nature conservation purposes (Rogers pers. comm.).
Seamount biota reflect patterns of nearest continental areas at high latitudes, whereas community structures depend on summit depth at lower latitudes (Wilson and Kaufmann 1987). Shallow (< 1000 m) seamounts represent equal proportions of regional and widespread species, while deeper seamounts are dominated by cosmopolitans. Latter authors considered that seamounts might provide stepping stones for the transoceanic and latitudinal dispersal of species. Endemism rates of particular seamounts were estimated to be 15.4% at maximum for invertebrates and 11.6% among fishes on a global scale with an increase in population divergence and speciation with increasing distance from continental margins and varying depths. Wilson and Kaufmann (1987) suggested four main biogeographic categories of seamount biota: provincial, widespread to cosmopolitan, endemic, and exotic.

Cold water coral reefs/bioherms of the ahermatypic reef-forming scleractinian species *Lophelia pertusa* and to a lesser extent other hard corals as *e.g. Madrepora oculata, Dendrophyllia cornigera*, and *Solenosmilia variabilis* are other special features of the intermediate deep seas and have attracted much attention to science because of their outstanding role and status in biology, ecology, and geology as well as because their recent threat from fisheries (*e.g.* Le Danois 1948; Tambs-Lyche 1958; Wilson 1979a, b; Zibrowius 1980; Frederiksen et al. 1992; Jensen and Frederiksen 1992; Mortensen et al. 1995; Freiwald 1998; Rogers 1999).
Hard substrate – at least a small solid piece as a pebble or a worm tube – and the presence of Atlantic oceanic water masses with temperatures between 4°-12°C seem to be requirements for *L. pertusa* to exist in the NEA (Tambs-Lyche 1958; Wilson 1979b; Freiwald 1998). For example in Norwegian fjords *L. pertusa* presence is restricted to such fjords that show an estuarine circulation (Fig. 18) with oceanic water influx at depths (Freiwald 1998). Within the OSPAR area *L. pertusa* has been recorded from the Azores area and all along the European continental margins with associated banks and seamounts from the Straits of Gibraltar to Finnmark in Norway (Rogers 1994). Only very few records were described from south of Iceland and the Iceland-Faeroes Rise, possibly indicating too low temperatures. Regarding the global scale of all records known so far, there is an overwhelming concentration in the NEA giving the OSPAR area global significance for this species. The bathymetric range of *L. pertusa* abundance stretches from nearly 2000 m at the Azores, ≥ 1000 m in the Bay of Biscay and Porcupine Seabight and Bank/West Ireland to 50 m in Norwegian and Swedish fjords with a main bathymetric presence between 200-400 m on the Scottish/Faeroese/mid-Norwegian shelves/slopes (Le Danois 1948; Frederiksen et al. 1992; Rogers 1999; Skjöld pers. com.). *L. pertusa* and other deep-water reef forming corals are often distributed on topographic highs as *e.g.* margins, pinnacles, ridges, and seamounts where currents support such suspension feeding organisms and sweep surfaces clear of fine sediments which might enhance settling (Frederiksen et al. 1992).
Providing a hard substrate in deep-water environments with several different microhabitats within a colony there is an enormous amount of species associated with reefs/bioherms of *L. pertusa* (Jensen and Frederiksen 1992; Mortensen et al. 1995; Rogers 1999). Being fragile in their structure *L. pertusa* and associated biocoenoses are severely vulnerable to impacts from *e.g.* fisheries or oil industry.

Hydrothermal vents (HTVs) are very special features within otherwise food-limited deep-sea environments depending on allochtonous input from surface waters. Catalysed by free living and endosymbiotic hyperthermophilic archaebacteria there have evolved communities entirely based on chemoautotrophic processes. 93% of the vent fauna (367 species/1998) are endemic to these ecosystem and new to science (Chevaldonné 1997; Tunnicliffe et al. 1998).
When seawater gets in contact with hot lava in the earths' crust at volcanic active locations, compounds as metal sulphides and methane derived from the reaction with crustal rocks at high temperatures are taken up to the seabed surface when the superheated water emerges again. Dissolved metal sulphides precipitate when cooled, forming large black clouds in the water and may build massive chimneys so-called "black smokers"

consisting of metal sulphides. At lower temperatures the sulphides mainly precipitate within the earths' crust rocks and fluids emerge cloudier as "white smokers". Reduced chemical compounds, mainly sulphides besides methane, are used by thermophilic chemlithoautotrophic archaebacteria as a source of energy to reduce carbon dioxide and assimilate organic carbon. Bacteria grow most abundantly in the shallow vent crust where upwelling hot, reducing hydrothermal fluid mixes with downwelling cold, oxygenated seawater. These chemolithoautotrophic bacteria can build mats on vent surfaces or form ekto- or endosymbiontic associations with certain invertebrates which depict the particular HTV fauna (JANNASCH and MOTTL 1985; GAGE and TYLER 1991; NICOLAS 1995).

The first HTV at the Azores Triple Junction was discovered only fairly recently in 1992 and discovery of further sites as well as knowledge about geological, geochemical, and biological peculiarities advanced only after 1993. The Menez Gwen field was discovered in 1994 (Saldanha 1996), while detection of the Rainbow field was in 1997, and of the Saldanha HTV field in 1998. Faunal communities at the Azores Triple Junction HTVs differ considerably from the HTVs TAG (26°N; 3625-3670 m depth) and Snake Pit (23°N; 3420-3480 m depth) that were detected further south on the MAR (outside the OSPAR area) earlier in 1985 or from Broken Spur (29°N; 3400 m depth) discovered in 1993 and depth was considered to be probably one shaping factor on geochemistry and biology (VAN DOVER 1995; SALDANHA et al. 1996). Deep-water and shallow-water HTVs show striking differences in their associated fauna with increasing pressure with depth providing effects on HTV chemistry and biology (ROGERS 1994).

So far four locations of hot deep-sea HTV fields are known within the OSPAR area (Fig. 107) at the Azores Tripel Junction (Chap. 3.1). Every field represents distinct geological, geochemical and ecological characteristics which have been summarised by SANTOS (2000). Comprehensively described these are from north to south:

Menez Gwen (37°51'N, 31°31'W): 855 m depth; $T_{max} \leq 281°C$; small chimneys and mounds consisting of white anhydrite – rich in baryte – and pillow lava around; located in a small summit graben of an axial high in the centre of the MAR segment; patchy mussel beds and some shrimp swarms besides other vent (35 species identified), or frequent commensalous or opportunistic fauna;

Lucky Strike (37°18'N, 32°16'W): 1620-1730 m depth; $T_{max} \leq 292°$-$333°C$; with 21 active chimneys – which are distributed around a fossil lava lake in the central caldeira of an axial volcano – it is one of the largest HTV fields along the MAR; sulphide structures are covered by mussel beds and *i.a.* shrimp patches at chimneys and fissures (highest biodiversity of HTVs at the Azores Tripel Junction: 66 species have been identified) besides other vent fauna;

Saldanha (36°56'N, 33°41'W): 2200 m depth; the active site is located in the axial discontinuity between the FAMOUS and AMAR segment of the MAR with fluids – which do not exit through chimneys but in a diffuse fashion directly out of the seafloor – not yet sampled; large water column methane anomaly; but yet no fauna only bacterial filaments were recorded;

Rainbow (36°14'N, 33°57'W): 2300 m depth; $T_{max} \leq 360°C$-$400 °C$; located in the axial discontinuity south of the AMAR segment it is one of the most active and the largest HTV fields along the MAR with about 10 groups of very active black smokers with chimneys and massive sulphides; 32 different species have been identified; fauna is shrimp dominated, with lesser abundance of mussels at areas of lesser activity; but the biomass is small and many chimneys have no animals;

SANTOS (2000) proposed a differentiation of four habitats related to hydrothermal activity at the Azores Tripel Junction according to temperature and substratum related faunal differences:

- Hot areas (100°-350°C) with sulphide substrates inhabited by bacteria and archaebacteria;
- Warm areas (20°-40°) of still hot sulphide chimney environments inhabited by shrimps (*Rimicaris exoculata, Mirocaris fortunata, Chorocaris chacei*), bacteria, and occasional gastropods (*Shinkailepas sp.*) and the crab (*Segonzacia mesatlantica*) on the lower limits;

- Colder areas (2°-20°C) on sulphide bedrock where fluids are less aggressive, inhabited by dominant mussel beds (*Bathymodiolus azoricus*) intermingled with commensalous polychaetes (*Branchipolinoe seepensis, Amathys lutzi*) and crabs (*Segonzacia mesatlantica*), partly covered by limpets (*Lepetodrillus sp.*), and with the gastropod (*Phymorhynchus sp.*) on the lower limits of this zone;
- Border areas without fluid influence with a character like the adjacent deep-sea but with more abundant fishes (*Cataetix laticeps*), crabs (*Chaceon affinis*), and apparently some sea urchins and sessile fauna (*e.g.* anthozoans) on rocky substrate.

Tunnicliffe et al. (1998) assumed a Pacific origin for Atlantic HTV fauna that could have spread through the Tethys Mediterranean Sea, but clustering allozyme and morphological data sets from bathymodiolid mussels from MAR HTVs, on the global scale the ones from the Atlantic differed considerably from those of the Gulf of Mexico or from the Pacific (Van Dover 1995). Also Gebruk et al. (1997) stated that there seem only few species to be common to both Oceans despite present knowledge of faunas from both Pacific and Atlantic black smokers is still poor.

Besides the outstanding status in deep-sea biology and evolutionary interests there has been stated a relative poverty in species diversity related to hydrothermal vents at both in soft sediments and on hard surfaces (Grassle 1989).

Shallow water and cooler HTV sites have been recorded from the Steinahóll (Grimsey) vent field (250-350 m depth) on the Reykjanes Ridge south-west of Iceland (*e.g.* German et al. 1993) and from the Kolbeinsey Ridge (70°-110°C; 100-106 m depth) north of Iceland (*e.g.* Fricke et al. 1989; Van Dover 1995) (Fig. 107). These HTV sites do show only communities of thermophilic chemoautotrophic archaebacterial mats, and opportunistic boreal megafauna (Fricke et al. 1989), but yet no higher taxa of typical HTV species have been detected (Van Dover 1995; Gebruk et al. 1997).

In addition to the southern MAR sites further hydrothermal activity was assumed in the deep Norwegian-Greenland Sea on Mohns Ridge (2600-2660 m depth) from detection of a density plume associated with fresh sheet and pillow basalts, hydrothermal sediments, minor temperature anomalies, and unusual abundance of sponges (Fig. 107) (Van Dover 1995) and at the Tjoernes Fracture Zone north of Iceland (Scholten et al. 1999).
Further hydrothermal sites in the Arctic part of the OSPAR area were detected with a submarine volcano on the Knipovich Ridge (76°48'N, 3500 m depth) in the northern Norwegian Sea (Pedersen and Sundvor 1998; Sundvor 1997) besides the "Haakon Mosby Mud Volcano" (72°N, 1250 m depth) which is part of the Bear Island submarine fan complex on the western Barents Sea continental slope (Vogt et al. 1997).
The hydrothermal activity on the Knipovich Ridge was indicated by near bottom temperature anomalies near the north flank of the submarine volcano, the presence of low-temperature hydrothermal mineralisation, Fe-Mn oxyhydroxide crusts on dredged basalts, and hydrothermal mound-like structures detected by camera at the rift valley (Pedersen and Sundvor 1998; Sundvor 1997) and by the presence of archaebacteria and bacteria in basalt from this low-temperature hydrothermal site (Thorseth et al. 1995).
The "Haakon Mosby Mud Volcano" shows temperature anomalies in the water column directly above the volcano centre while emitting thermal and dissolved methane plumes. Sediment cores of the centre are rich in hydrogen sulphide gas and methane hydrate crystals. Methane hydrates are scattered across the sea floor in small fragments and extensive patches and numerous tube worms in the sediment were observed by video. Further examinations showed that microbial methane oxidation forms the base of the food chain of a benthic community which is dominated by two species of pogonophorans with endosymbiotic methanotrophic bacteria and probably attracting populous demersal fishes at this site (Vogt et al. 1997).

There is a discussion about palaeotectonic controls of HTV biogeography also concerning the recent biogeographic differentiation between vent sites of different segments on the MAR. Ongoing discussions concern faunal relations of Atlantic sites south of the Greenland-Iceland-Faeroe Rise, of putative or detected low-temperature vent sites on the Arctic ridges, and faunal communication and biogeographic interrelations with the Pacific sites through the Arctic or the Tethyan Central American connection or regarding putative

South Atlantic vent sites that may have seeded Atlantic HTV fauna from the proto-Indian Ocean (VAN DOVER 1995; TUNNICLIFFE et al. 1998). Interesting in this sense is the detection of fossil hydrothermal pyrite chimneys with a fossilised worm assemblage in Ireland dated to an age of 350 mio years (BANKS 1985) (comp. development of the Atlantic by seafloor spreading, Chap. 3.1). BANKS (1985) was not able to identify the worm taxonomy, but it would be of particular interest because presently there are no living vestimentiferan tube worm assemblages known from Atlantic/MAR HTVs unlike their present dominance at HTVs in the Pacific (GEBRUK et al. 1997).

Other geochemically driven communities are those of so called **cold seeps** which are another deep-sea reducing habitat. These much less characterised deep-sea chemosynthesis-based autotrophic communities are fuelled by chemoautotrophic endosymbiontic bacterial oxidation of geogenic or biogenic methane rich fluids, oxidation of sulphides, or sulphate reduction coupled with methane oxidation by thiotrophic bacteria. Composition and origin of fluids are various on passive margins with liquid (crude oil), gas, and solid (methane hydrate) phases, while on active margins methane rich fluids are related to the thermogenic or biogenic decomposition of matter. (Gas hydrates are only stable in their solid phase in the low temperature-high pressure environment of the deep seafloor.) Dominating higher cold-seep symbiont-containing species are bivalves, pogonophores, sponges of which are a large majority endemic to a seep area. The symbiont-containing species are mainly endemic to the cold-seep ecosystem and a biodiversity as high as at HTVs was detected at several seeps (SIBUET and OLU 1998). Since there is no active geological subduction zone in the OSPAR area latter authors did not give a cold-seep account for the OSPAR area, whereas GEBRUK et al. (1997) and GUBBAY (1999) cited some endosymbiont bearing organism records in pockmarks and seeps in the shallow North Sea and in the Norwegian deep trough especially in the Skagerrak. In addition methane hydrate based communities were recorded from the "Haakon Mosby Mud Volcano" in the deep Norwegian Sea, as described above.

These cold-seeps – together with other deep-sea reducing habitats as wrecks, large (*e.g.* whale, tree) carcasses, and sunken organic waste lumbs – are considered to be probably stepping stones for larval stages and the oceanic dispersal of some HTV species (GEBRUK et al. 1997; TUNNICLIFFE et al. 1998; BETT pers. com.).

In addition to the extraordinary biota described above, there are occasionally brine seeps with specialised biocoenoses in the deep-sea. Furthermore, living bacteria were discovered in deep subsurface sediments several 100 m below the ocean floor (GAGE and TYLER 1991).

Looking at general deep-sea patterns however – still lacking sufficient information on deep-sea species and their spatial and temporal distribution patterns – marked differences in composition of biocoenoses were described only between the deep waters of the Arctic including the Norwegian-Greenland basins and the remaining North-East Atlantic concerning the OSPAR area. Thus, it might be yet too uncertain to split off parts of the North Atlantic Abyssal Province for the designation of an additional West Atlantic Abyssal Province and an additional East Atlantic Abyssal Province as did VINOGRADOVA (1979) (Fig. 80), a combination of a West-European and a East Atlantic/Lusitano-Mauretano-Mediterranean with a North Atlantic bathyal unit as shown by ZEZINA (1997) (Fig. 79), or a segregation of biogeographic units related to different trophic situations (SOKOLOVA 1997) (Fig. 103).

COX and MOORE (2000) stated that it is impossible to identify different biogeographic areas upon the deep-sea floor of a single ocean, or even to draw up lists of faunal differences between one ocean and another, due to still deficient information on deep-sea benthos.

The partly contradictory information and considerations argued above resulted in a classification of an **Atlantic region** with an **Arctic** and an **Atlantic subregion** in the deep OSPAR area. The latter with a **North Atlantic province**. The most striking factor for the determination of deep-sea species distribution patterns is the temperature difference on either side of the Greenland-Iceland-Faeroe-Scotland Rise. Regarding this differentiation, the **emergence of deep-sea species in cold shallow waters of the Arctic** as mentioned in the chapters 3.2 and 6.2 has to be kept in mind.

Regarding other properties than endemism rates, further subdivisions of the deep North-East Atlantic and Arctic might be possible. Subdivisions to the north and south of Fram Strait and between eutrophic temperate and at oligotrophic oceanic regions due to different production regimes in the epipelagial above as well as below upwelling areas off the Iberian coast or off the West-European continental slope for a diversified input of nutrients might be discussed.

6.4 Scheme and maps of the hierarchical biogeographic subdivision of the North-East Atlantic and Arctic Oceans within the boundaries of the OSPAR area

The following classification scheme has been elaborated according to considerations given above, an extensive evaluation of biogeographic references exceeding the frame of this study, and diverse personal communications.

This scheme shows the hierarchical relationships, affinities, and the fitting into the context within the entire Atlantic-Arctic Ocean realm system, for a clarification of terms see chapter 6.1. Where existing, the traditional names have been used to name the different biogeographic provinces. Water masses correlated with biogeographic patterns have been used for structuring the different entities because single taxonomic/species relations would not be of use for the description of the entire OSPAR area in this integrated approach.

Overall important is to bear in mind that delimitations marked on the following maps are never sharp biological distribution limits (there are only very rare exceptions) but in most cases gradual transition zones with only more or less distinct discontinuities in the replacement of species within the biocoenoses. This applies especially to the transition areas along the Lusitanean-Boreal transition along the western approach to the British Isles and the Wyville Thomson Ridge-Faeroe Bank area, the Boreal-Subarctic transition belt from Iceland, the Faeroes, Shetlands to along the Norwegian coast, and in the Finnmark-Barents Sea-White Sea area.

Concerning the biogeographic maps it should be noted that there is a different western boundary in the western Barents Sea for the benthic and the pelagic realms.
The Azores, that are an oceanic island archipelago of volcanic origin (Chap. 3.1), do not have a shallow continental shelf but relatively steep slopes. Thus, as "emerged seamounts", vertical patterns are more comparable to this oceanic feature. Even though not connected by a shelf platform they form nevertheless one biogeographical unit together (Figs. 105, 106).
The cooler Irish Sea waters could not be delineated against surrounding warmer waters in the pelagic map due to graphical problems in the colour graduation.
The hydrothermal vent at Mohns Ridge (Fig. 107), so far known, is still putative as described in chapter 6.3.3.

(HOLO)PELAGIC biome (< 1000 m depth)**:**

Atlantic region

East Atlantic Temperate subregion:
water masses/pelagic provinces: Warm-temperate waters
water masses/pelagic provinces: Cool-temperate waters

Arctic region (no further subdivision in subregions and provinces)
water masses/pelagic provinces: Cold-Arctic waters

BENTHAL and **NERITOPELAGIAL** of the **SHELF & UPPER CONTINENTAL SLOPE** (< 1000 m depth), and **ICE-COVER biomes:**

Atlantic region

East Atlantic Temperate subregion:

water masses: Warm-temperate waters
provinces: Macaronesia: Azores subprovince
Lusitanean
subprovinces: Cold Lusitanean, Warm Lusitanean (N and S)
Lusitanean–boreal

water masses: Cool-temperate waters
provinces: Boreal-lusitanean
Boreal
Norwegian Coast
subprovinces: Finnmark, Westnorway, Skagerrak
South Iceland – Faeroe Shelf

Arctic region
water masses: Cold Arctic waters
provinces: High Arctic Maritime
North-East Greenland Shelf;
South-East Greenland – North Iceland Shelf
Barents Sea
subprovince: White Sea

DEEP-SEA biome (pelagial and benthal > 1000 m depth)**:**

Atlanto-Arctic deep-sea region

Atlantic subregion
province: North Atlantic province (water masses: ~ 2°-8° C)

Arctic subregion (water masses: < 0° C)
province: no further subdivision within the OSPAR area

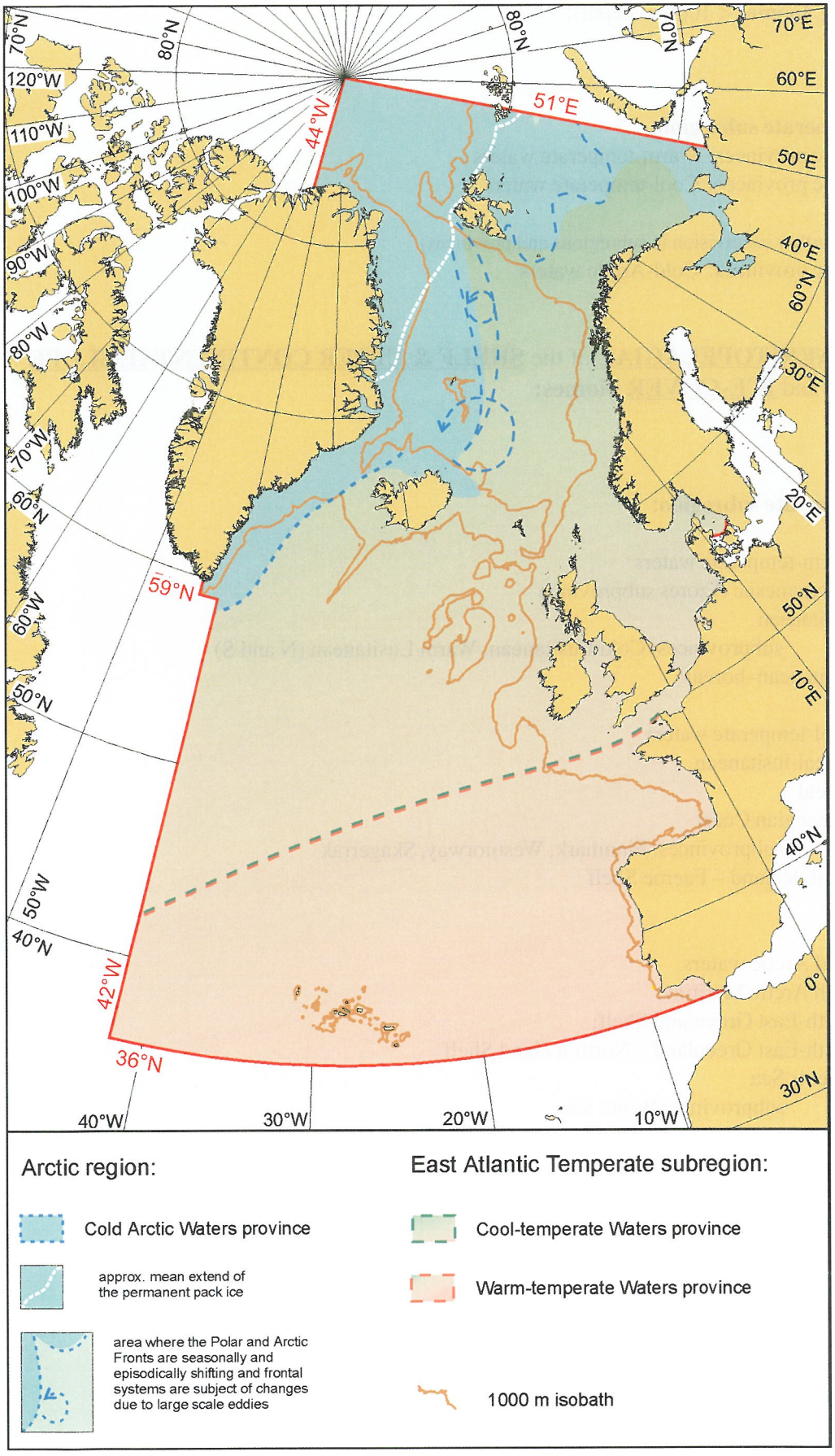


Fig. 104: Biogeographic classification of the **pelagial** (< 1000 m depth) of the OSPAR Maritime Area. The 1000 m isobath segregates the neritopelagial from the holopelagial.

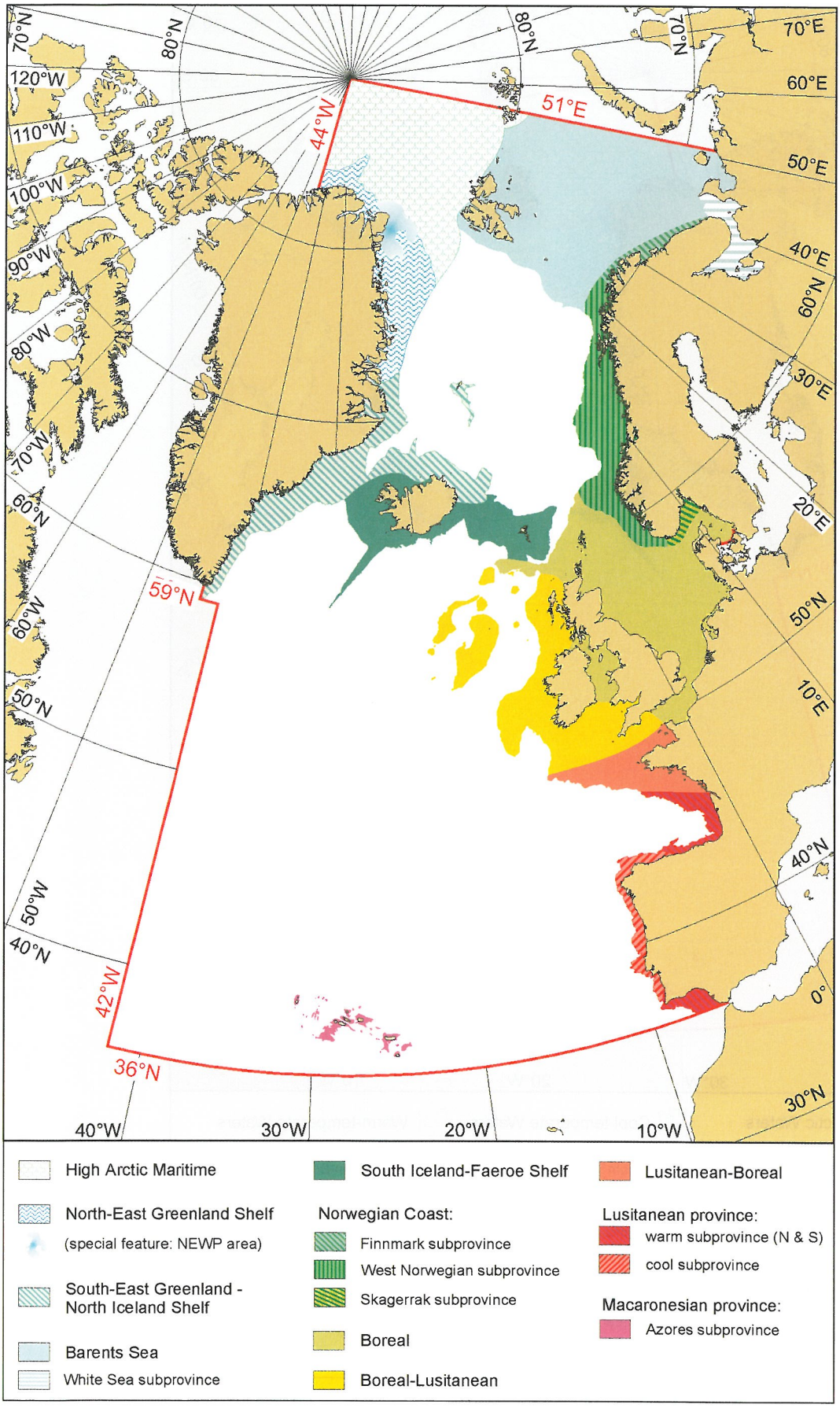


Fig. 105: Biogeographic classification of the **benthal** and **neritopelagial** of the **shelf** and **upper continental slope** (< 1000 m depth), and **ice-cover** biomes of the OSPAR Maritime Area.

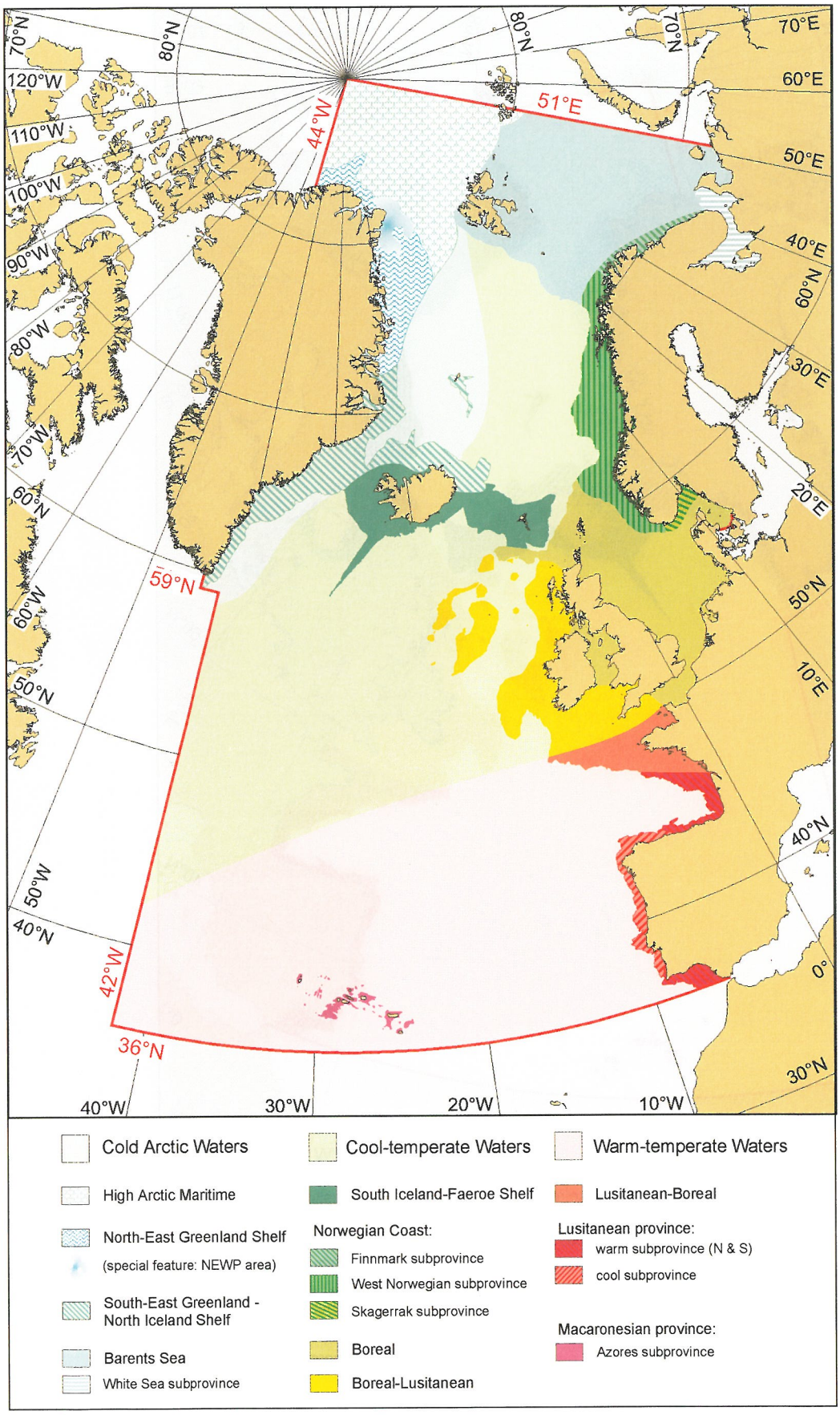


Fig. 106: Biogeographic classification of the **benthal** and **neritopelagial** of the **shelf** and **upper continental slope** (< 1000 m depth), and **ice-cover** biomes combined with the superordinate **holopelagic** provinces (< 1000 m depth) of the OSPAR Maritime Area.

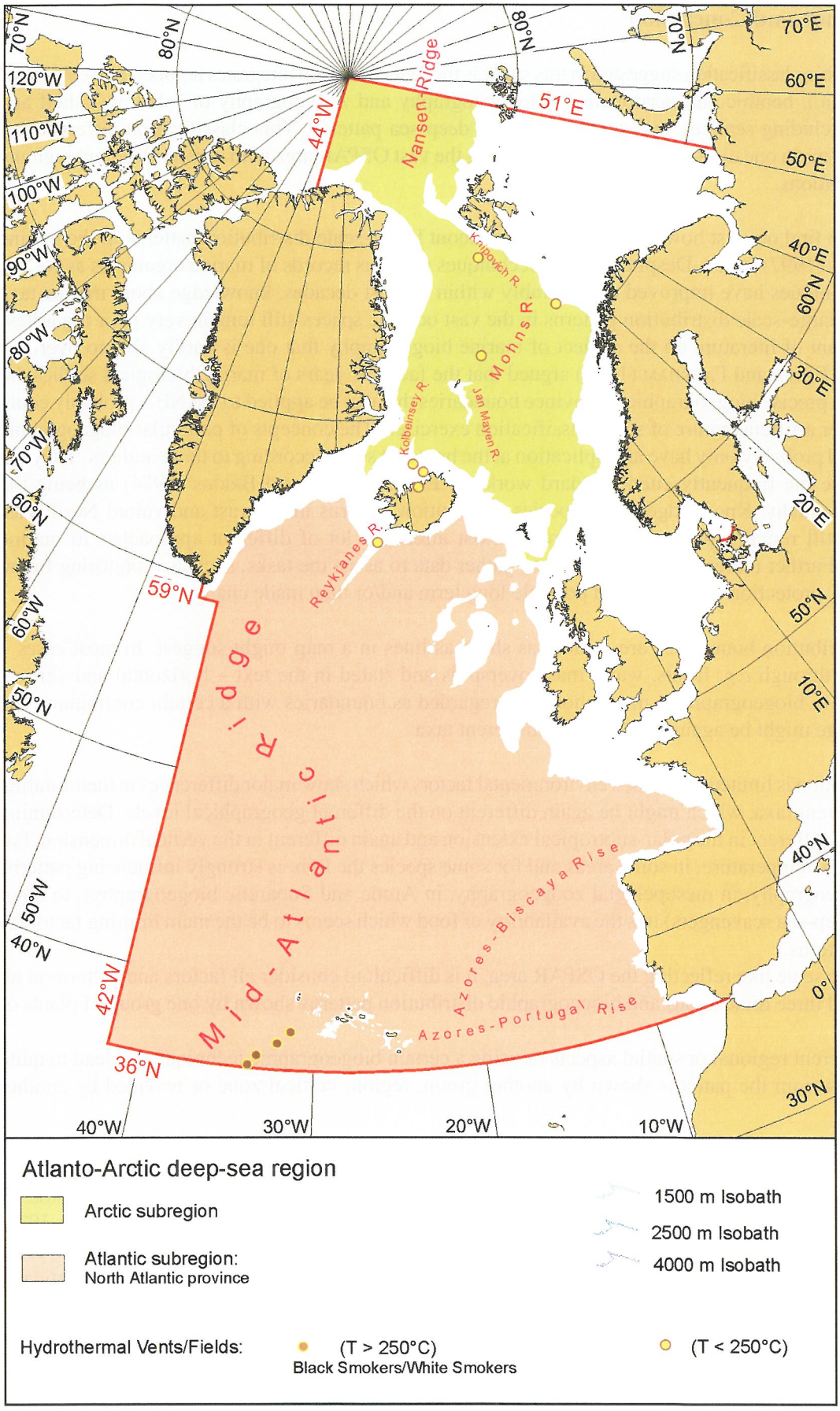


Fig. 107: Biogeographic classification of the **deep-sea** (pelagial and benthal > 1000 m depth) of the OSPAR Maritime Area with some selected isobaths and features shown.

7 Discussion and Conclusion

The biogeographic classification suggested in this study is the first one which integrates holopelagic (epipelagic and mesopelagic), benthic and neritopelagic phytogeography and zoogeography of "shallow" shelf and slope zones (including sea ice), and zoogeographical deep-sea patterns. This classification differentiates three major realms in one classification system covering the vast OSPAR area with its very different regional and spatial situations.

It is sobering to find out just how little is still known about larger-scale distribution patterns in the marine realm as CRAME (1997) stated. Despite research techniques and thus records of marine organisms as well as evaluation techniques have improved considerably within the last decades, knowledge about marine taxa and especially large-scale distribution patterns in the vast oceanic spaces still remain very poor regardless that huge amount of literature on the subject of marine biogeography that one is hardly able to overlook (BRIGGS 1995). EARLL and FARNHAM (1983) argued that the fact that years of marine biological studies did not prolifer any precise biogeographical province boundaries that can be applied to the NEA probably could reflect the rather artificial nature of such classification exercises. The concepts of particular biogeographic provinces could probably only have an application at the broadest scale according to these authors. They did right to criticise the frequently cited standard works of EKMAN (1953) and BRIGGS (1974) as being too superficial and patchy. Knowledge about species distribution patterns in the vast and varied North-East Atlantic area still remains poor even if there do exist already a lot of different approaches to marine biogeography. Further research has to be done to gather data to assist the tasks, such as monitoring future protected areas, protection measures, and possible long term and/or man made changes.

Biological distribution boundaries are seldom as sharp as lines in a map might suggest. In most cases – except created through *e.g.* fronts, water mass overspills and stated in the text – horizontal and vertical boundary lines in biogeographical maps should be regarded as boundaries with a certain continuum. The degree of change might be again different with different taxa.

Species distribution is limited by various environmental factors which show major differences in their limiting effects on different taxa, which might be again different on the different geographical levels. Determining factors are very different in the polar-subtropical extension and again different in the vertical dimension. For most species it is temperature, in some areas and for some species the light is strongly influencing patterns (*e.g.* in phytogeography, in mesopelagial zoogeography, in Arctic and Subarctic biogeography), to other species (*e.g.* deep-sea scavengers) it is the availability of food which seems to be the main limiting factor for distribution patterns.
Thus, on a large scale like reflecting the OSPAR area, it is difficult to consider all factors and patterns at all sub-scales in all three dimensions and biogeographic distribution patterns shown by one group of plants or animals.
Regarding different regional or spatial aspects or using a certain biogeographic technique can lead to quite different results from the patterns shown by another group, region, vertical zone or revealed by another technique.

Marine macrophytes are fixed in their location, they grow along coastal fringes and are vertically distributed only down to sublittoral depths. Thus, the description of seaweed and seagrass distributions (*e.g.* BØRGESEN 1902, 1908; BØRGESEN and JÓNSSON 1905/1908; DAVY DE VIRVILLE 1940; DEN HARTOG 1970; IRVINE 1974, 1982; IRVINE et al. 1982; GALLARDO et al. 1985; SOUTH and TITTLEY 1986; BREEMAN 1988; TITTLEY et al. 1982, 1985, 1989; LLORIS et al. 1991; and references therein) is somewhat more easy to analyse statistically than the distribution of mobile organisms in vast and dynamic oceanic spaces. VAN DEN HOEK (1975) even stressed that seaweed biogeography can be more easily investigated compared to land flora biogeography because of the fringing and linear character of seaweed distribution along the coasts in contrast to plane terrestrial plant distribution. Phytogeographical results are therefore less contradictory than biogeographic maps produced for various faunas associated with different ecological biomes.

There is a discrepancy in views of planktologists and benthologists about a delimitation between the warm temperate/subtropical and cool temperate/boreal units within the NEA. While many benthologists seem to prefer a boundary at the western English Channel there were been presented biogeographic classifications and maps mainly of ecologically orientated (nutrient based) pelagic works (*e.g.* VINOGRADOV 1968; BERGER 1974; HERMAN 1979; PIERROT-BULTS and VAN DER SPOEL 1979; PRUD'HOMME VAN REINE and VAN DEN HOEK 1990; ANGEL 1991; LONGHURST 1998) that show or mention a boundary between warm temperate/subtropical and cool temperate/boreal units at about 40° N in the NEA. Especially ANGEL (1991) stressed this pelagic boundary at 40°N and referred to satellite images where it should be clearly marked. However on the satellite image provided by LONGHURST (Figs. 96-99) this boundary appears only in spring and far less pronounced in autumn. Conversely there is evidence for certain discontinuities on the latitude of the English Channel entrance (*e.g.* FORBES and GODWIN-AUSTEN 1859; FISCHER-PIETTE 1936; EKMAN 1953; CRISP and SOUTHWARD 1958; HOLME 1961, 1966; BACKUS et al. 1977; BEKLEMISHEV 1977; FLEMINGER and HULSEMANN 1977; MICHANEK 1979; EARLL AND FARNHAM 1983; HAYDEN et al. 1984; GOLIKOV et al. 1990; BRIGGS 1974, 1995; GUBBAY 1988, 1995a; OKOLODKOV and DODGE 1996; SEMINA 1997; HISCOCK 1985, 1991, 1998) while MCINTYRE and BÉ (1967) and ANGEL (1979b) marked both boundaries. ANGEL (1979b), ANGEL and FASHAM (1975), and FASHAM and FOXTON (1979) presented more differentiated schemes of various pelagic boundaries related to different species groups and water masses in a vertical cross-section between 10°N and 60°N. However boundaries/zones were not the same for ostracods and decapods. To achieve a consistency and congruency between the classifications for the holopelagial on the one hand and the neritopelagial and benthic coastal units of the southern OSPAR area for which evidence was given in this study on the other hand, I set the boundary at the latitude of the English Channel entrance. Both delimitations might be somewhat arbitrary for the holopelagial due to a more gradual change in oceanic temperate waters but the difficulty of "drawing lines in the water" had to be tackled somehow.

BACKUS et al. (1977) and LONGHURST (1998) and some other research on the pelagial (*e.g.* some maps of VAN DER SPOEL and HEYMAN 1983) classified the very south-eastern corner of the pelagial of the OSPAR area as belonging to a "mid-oceanic unit" of the northern Atlantic subtropical gyre. Such a separation might be possible since this area lies in an oligotrophic region just in-between the NAD and a large scale meander of the northern branch of the Azores current that gives this area probably a different character. But this was not considered to make sense because the area is rather small and this classification should distinguish practical biogeographic units.

As EARLL and FARNHAM (1983) and HISCOCK (1998) had set out, there had been only limited sampling by dredges on soft substrate seafloors or in very shallow littoral environments concerning biological records of the benthal before the introduction of scuba diving. Deeper hard bottoms had to be left out in past! Many biogeographic classifications however had been elaborated before or used data that had been gathered before. With the use of modern diving techniques and remotely operated sensor and sampling techniques our view and existing biogeographic descriptions might get enhanced, renewed, or possibly even changed when all new data will be reviewed and compared with the old ones.

In this study the Barents Sea has been designated as one unit despite the northern and south-eastern stretch of this province having different ice regimes and also different benthic biocoenoses. Thus, the shallow stretch between Spitzbergen and the Franz Josef archipelago, being nearly permanently ice covered but lying above the West Siberian continental shelf unlike the High Arctic Maritime Province, could otherwise be designated as being a part of a "High Arctic shallow marine province" as did ZENKEVITCH (1963). This would also correspond with the delimitation between the marine Arctic and Subarctic regions of DUNBAR (1985) and remarks of GOLIKOV et al. (1990). But regarding the arbitrary OSPAR boundary in this region and reflecting the need for a practical number of biogeographic units (Chap. 1) the northern and south-eastern parts of the Barents Sea have not been split off.
Similar reflections apply to the (nerito)pelagic subdivision of the Barents Sea. Being rather a region of transition between the seasonal changing influence of warm waters from the Norwegian current and cold arctic waters contrasting boundaries between pelagial and benthal are difficult to define (see Chaps. 6.3.1; 6.3.2). Actually there is a south-western part which is more influenced by the warm descendants of the NAD

and northern, eastern, and south-eastern parts that are influenced by cold Arctic waters and fluctuating ice covers (Fig. 4.3). Such differences are reflected in the classification of LONGHURST (1995, 1998; Chap. 5.1.13) with his delimitation between his Boreal Polar Province and Atlantic Subarctic Province. Also abundance patterns of sea mammals as *Megaptera novaeangliae* (humpback whale) and *Phoecena phoecena* (harbour porpoise), both with cool temperate Atlantic-Subarctic distributions and *Monodon monoceros* (narwhale) and *Delphinapterus leucas* (white whale) both with cold Polar-Arctic distributions given by RIDGWAY and HARRISON (1985, 1989) and HANSEN et al. (1996) indicate such a subdivision.

The southern subprovinces of Norway and the South Iceland-Faeroe province as delimited in this classification have close affinities to the character of the Boreal province as classified together by *e.g.* EARLL and FARNHAM (1983) or BRIGGS (1974, 1995). Others joined a belt from south Iceland over the Faeroes and Shetlands to the south and middle of Norway and named it Boreal(-Arctic) province (FORBES and GODWIN-AUSTEN (1859); HISCOCK (1998), Scandinavian province (GOLIKOV et al. 1990), or Atlantic Subarctic province (BACKUS et al. 1977).
In fact this area is a transition area between cool-temperate and boreal-arctic species distribution areas but with a horizontal boundary which is difficult to delimit. In this region cold-stenotherm forms are to be found at greater depths than more eurytherm boreal organisms thus making a horizontal discrimination even more difficult due to this vertical differentiation. But the (sub)provinces, as classified in this study, still have peculiarities that make them different as described in chapter 6.3.2. A segregation of those provinces depends on the scale of biogeography and criteria for the classification.

The areas along the Norwegian coast have been assigned by GLÉMAREC (1998/2000 pers. comm.) on the base of bivalve distributions to his cool temperate and mild temperate provinces to the north and south of the Trondheim Fjord (~ 64°N) with a possible further Subarctic subprovince north of the Lofoten Islands. However BRATTEGARD and HOLTHE (1995) took much more groups of marine organisms into account for their subdivision, thus I followed their delimitations for my classification.

The classification of the area between the Gironde estuary and St. Jean de Luz in the south-eastern corner of the Bay of Biscay (Gulf of Gascony) might be further discussed. According to GLÉMAREC (1998/2000 pers. comm., see also DAUVIN 1997) it belongs to his mild temperate province and the Bay of Biscay should be a whole with larger-scale differences in benthic substrate characteristics creating artefacts. In contrary the mouth of the Gironde has been characterised as a biogeographic boundary by CRISP and FISCHER-PIETTE (1959), SOUTHWARD (1985), GUBBAY (1995), and HISCOCK (1998).

Concerning the deep-sea there was paid more attention to questions of vertical zonation of distribution patterns and to problems of the trophic situation (C-, N-, and energy fluxes) in the past than to a horizontal differentiation of the distribution of deep-sea taxa. It will be hercules task to explore and describe differences in bathymetric patterns in species' ranges at different latitudes with an accurate delineation as GAGE and MAY (1993) considered and THURSTON et al. (1998) argued that deep-sea biogeographic patterns remain subject to speculation.
There had been taken a single vertical boundary for a subdivision of the biogeographic classification of this study for practical purposes. A lot of evidence for a vertical biogeographic boundary at about 1000 m depth between shallow and deep-sea organism assemblages has been given in chapter 6.2 for temperate as well as for Arctic regions. The vertical boundary of 1000 m was used also for the high latitude and Arctic units despite the phenomenon of polar emergence. AAGAARD et al. (1985) described a pronounced influence of Atlantic water masses down to depths of close to 1000 m in the northern seas and also Svavarsson et al. (1993) highlighted a vertical discontinuity in species compositions at ~1000 m in the Norwegian-Greenland Sea.

For the horizontal classification of the deep-sea there exist still quite contradictory and varying descriptions. For example SOKOLOVA (1997) (Fig. 103) emphasises a longitudinal subdivision of the NEA at ~20°W in contrast to MERRETT (1987); THIEL (1983); THIEL et al. (1989); RICE et al. (1994); THURSTON et al. (1994, 1995, 1998); .... who stress otherwise a latitudinal segregation between eutrophic and oligotrophic regions at

~40°N. For this study have been designated only two major units for reasons given above and contradictory and still insufficient information about deep-sea patterns.
Further subdivisions of the "Arctic subregion" and the "North Atlantic Province" due to a different character of pelagic marine snow/phytodetritus and therefore a different input of nutrients in areas with a high productivity below upwellings and closer to the shelf/continental slope might be possible. In the sense of ongoing discussions about the importance of the trophic situation for deep-sea distribution patterns (*e.g.* BILLET et al. 1983; THIEL 1983; SIBUET 1985; MERRET 1987; THIEL et al. 1989; ETTER and GRASSLE 1992; REX et al. 1993; RICE et al. 1994; BRIGGS 1995; LAMBSHEAD et al. 1995; LAMPITT and ANTIA 1997; MERRET and HAEDRICH 1997; REX et al. 1997; VINOGRADOVA 1997; ZEZINA 1997; LONGHURST 1998; THURSTON et al. 1994, 1995, 1998; BETT pers. com.; THIEL pers. com.) there could be suggested the designation of an oligotrophic "High Arctic Deep-Sea Basin" north of Fram Strait as a subdivision of the "Arctic subregion" and additional subdivisions of the deep "North Atlantic Province". These could distinguish areas of higher nutrient input and therefore higher biomass, abundance, diversity and different assemblage compositions of deep-sea species north of a boundary at ~ 40°-45°N and oligotrophic oceanic abyssal areas to the south (comp. Figs. 69-99). Further subdivision could reflect a differentiation between "shelf/slope-influenced" bathyal areas and oceanic abyssal regions similar to VINOGRADOVA and ZEZINA (1998) (Chap. 5.1.27).

Besides spatial dimensions the time factor has to be taken into account. Biogeographical patterns aren't and have never been static. Changes in the designated biogeographical zones and biocoenoses described here may take place due to terms of evolution as well as related to global effects of manmade changes in the marine environment such as climate change and industrial fisheries. Alterations of currents, water masses, frontal and upwelling areas and therefore biogeographic fundaments have not only been reported from the "El Niño-Southern Oscillation" area in the Pacific but also from upwelling areas at the Iberian coast (WYATT and LARRAÑETA 1988; WYATT and PEREZ-GANDARAS 1989; SHERMAN 1992), according to the Russel Cycle in the Western English Channel (SOUTHWARD 1980), and from the "Great Salinity Anomaly 1968-1982" (DICKSON et al. 1988), with evidence from the East Greenland Sea (HOVGÅRD and BUCH 1990), as well as from the Barents Sea (BLACKER 1957; BLINDHEIM and LOENG 1981; LOENG 1987; MIDTTUN and LOENG 1987; SKJOLDAL and REY 1989; BLINDHEIM and SKJOLDAL 1993; ANKER-NILSSEN 1996), the White Sea (GOLIKOV et al. 1990) and the entire Arctic (ZENKEVITCH 1963).

The construction of ocean-connecting channels (Suez-Canal; Panama-Canal; Rhine-Danubian-Canal; Baltic Sea-Volga-Don waterways) has opened pathways that connect the North Atlantic with the Indian and Pacific Oceans as well as with the Caspian Sea for marine, brackish-euryhaline, anadromuous or katadromuous organisms. Together with an increased shipping around the globe, anthropogenic dispersal of organisms beyond their natural boundaries might result in a fading of distinct biogeographic patterns, original biocoenoses, and partly in a decrease of original species abundance due to competition advantages of invaders. Neobiota abundance has increased considerably within the last ~ 150 years in European waters. (*e.g.* EKMAN 1953; CRISP 1958; POR 1978; VERMEIJ 1978; FARNHAM 1980; BARNES and HUGHES 1988; COSTELLO et al. 1996; ENO et al. 2000).

The physio-oceanographic concept of DAY and ROFF (1999) (Chap. 5.1.4) is one of the few approaches that tries to reflect benthic and pelagic environments in all three dimensions. The applicability of this concept and whether the expected communities are really found in the physiographically defined units has still to be proven. Some details of their concept does not seem to be applicable to a wide area such as the OSPAR area which also includes warm-temperate regions. Their concept might not be able to cope with very fluctuating (seasonally and episodically) environments as *e.g.* the Barents Sea concerning all levels and the six fixed depth intervals do not necessarily reflect biological patterns. In addition, depth patterns are much different *e.g.* off the Straits of Gibraltar, on the MAR, in the Rockall Trough, and on the continental slope north of Svalbard (Spitzbergen) or on the continental slope north of Greenland in the Arctic basin.
However, the classification concept seems to be quite valuable to be used for a marine classification on marine landscape/seascape-feature level (see LAFFOLEY et al. 2000a, b) and community level between biogeographic subprovinces and habitat classifications as *e.g.* presently prepared with BioMar or the EUNIS.

Ecological geography as described by planktonic and productivity patterns (LONGHURST 1998) might enhance the ideas of pelagic patterns and even habitats considerably (*e.g.* oceanic and shelf-sea fronts as ecotones; the shallow pycnocline as habitat and boundary) but as cited by LONGHURST (1998) in the image of rain forests in Brazil, Papua-New Guinea, and the Congo being ecologically quite similar but taxonomically totally different, this problem would also apply to many biogeographically different but ecologically similar (similarly productive) marine regions.

With regard to future work the evaluation and integration of satellite images, *e.g.* showing the character and distribution of ice, plankton, salinity and energy flows, and new oceanographic techniques as *e.g.* multibeam scans could be useful. However, difficulties in the meso-scale classification of large ocean areas by satellite images are obvious, as *e.g.* visible in the figures 96-99 (Chap. 6.3.1).
But combined with species distribution data and transferred into a Geographic Information System (*e.g.* ERMS, OBIS), such tools would provide a temporal, continuous, and area covering monitoring and make the designated units more precise (see also Chap. 8). Also effects of protection measures in the vast OSPAR area could possibly be surveyed by using these tools.

The question remains whether further subdivisions of this classification are suitable for the purposes of the OSPAR-convention (see Chap. 1).
To fill the gap between the provinces/subprovinces of this biogeographical classification and the recent work on a hierarchical habitat classification within OSPAR/EUNIS/ICES further subdivisions of already identified biogeographic units on additional meso-scale classification levels should be made related to oceanographic features as

- *e.g.* related to lower levels of the classification system of DAY and ROFF (1999) (Chap. 5.1.4);
- to lower levels of the comparative scheme of EARLL and FARNHAM (1983) (Fig. 6.1.5);
- marine landscape/seascape-feature level of LAFFOLEY et al. (2000a, b);

or additionally related to these proposed features:

- clusters of benthic substrates on meso-scale level *e.g.* derived from multibeam scans predicting meso-scale benthic communities on this basis and integrating existing meso-scale benthic community classifications (*e.g.* SALZWEDEL et al. 1985; GLÉMAREC and BAYED 1987; MACKIE 1990; REISE and BARTSCH 1990; KRÖNKE 1992; KÜNITZER et al. 1992; GLÉMAREC 1973, 1995; MACKIE et al. 1995; HISCOCK 1991, 1995, 1998);
- meso-scale fronts (*e.g.* PINGREE and GRIFFITH 1978), eddies, mixing (*e.g.* PINGREE 1978), stratification (*e.g.* PINGREE et al. 1976), convergences, divergences, turbidites;
- nutrients and productivity patterns.

8 Outlook

Reflecting the complexity of marine biological distribution patterns a modern marine biogeographic classification that covers the OSPAR Maritime Area or the entire European seas in a consistent and comparable way is still missing. Such a categorisation should integrate patterns of all marine taxa (flora and fauna) in all three-dimensioned spatial magnitudes to describe the frame of Europe's marine biodiversity.

In future times distribution patterns might change faster than so far either due to an increase in climate change and by natural or anthropogenic dispersal and human impacts. Dispersal of species is an everyday occurrence and inexorable continuing process but some anthropogenic activities, *e.g.* industrial fisheries, discard of bilge water, deliberation of genetically manipulated organisms, and intentional deliberation have had already their impacts on patterns of biodiversity.

New records of species also raise the question as to whether they have been introduced (when? from where?) or whether they represent natural extensions in range or have always been present but undetected (EARLL and FARNHAM 1983; Thiel pers. com.).

With the development of digital databases a freer exchange of biogeographic information will be facilitated, provided data-sets and formats are compatible with each other (KRAUSE and ANGEL 1994). Extensive marine biological databases exist for example with the European Register of Marine Species (ERMS) of the MAST/ EU (http://erms.biol.soton.ac.uk/), the North-East Atlantic Taxa (NEAT) project of the Tjärno-Marine Biological Laboratory/Sweden for marine invertebrates (http://www.tmbl.gu.se/libdb/taxon/taxa.html), or at Norway's "Direktoratet for Naturforvaltning" (BRATTEGARD and HOLTHE 1995, 1997; GULLIKSEN et al. 1999). The second stage of the ERMS project and the Ocean Biogeographic Information System (OBIS) of the Rutgers University/ New Jersey, USA (http://www.imcs.rutgers.edu/OBIS/index.html) are first attempts for the tremendous task to join such taxonomic data with geographical references which, when sufficient complete, could be used for biogeographic statistics, computing of three-dimensional distribution schemes and, production of customised maps for general or specific applications. Besides traditional approaches for research and description of the world's biosphere and more modern application-related biogeographic approaches for *e.g.* purposes of marine nature conservation and resource management, future applications could integrate the phenological monitoring and documentation of "global climate change" effects on the marine environment, provided methods of research as well as data presentation are comparable and temporal data-sets are of sufficient duration to exclude short-time fluctuating effects.

High species diversity in the pelagial is commonly associated with regions of low productivity that lack strong seasonality in the production cycle but also with the confluence of different water masses in highly productive frontal zones (ANGEL 1993). For the case that species diversity is considered as a principal criterion for nature conservation strategies, these strategies have to realise that a broad biological diversity is linked to ecological processes and often related to a lower trophic status as described above. But on the other hand, nature conservation strategies should also aim at the protection of highly productive areas with probably lower diversity that suffer most from overexploitation.

Protection measures are advised also for the deep-sea, an area that is out of mind of most conservationists. Species, threatened relatively new but already most at risk, include mesopelagic and slope fishes (as *e.g.* ling, blue ling, tusk, roundnose grenadier, black scabbardfish, orange roughy, red sea bream, and deep-water sharks) with long lasting juvenile stages before their first reproduction. Since many of the stocks concerned extend beyond national waters or EEZs international conservation action is demanded (*e.g.* SAR bulletin 21.4/2000).

With regard to the intended purpose of this study to be used within a framework of implementing *i.a.* MPAs concerning Annex V of the OSPAR convention it should be noticed that species at limits of their geographical distribution range may be especially vulnerable to environmental (natural and anthropogenic) stress.

9 Summary

This paper presents a description of oceanographic features that influence marine biogeography of the North-East Atlantic and the adjacent Arctic Ocean, a broad review of existing different approaches to marine biogeography concerning *i.a.* the OSPAR area, and a resulting synoptical biogeographical classification of the OSPAR area on different hierarchical levels.
This classification is the first to integrate different pelagic, shallow water benthic and neritic, ice-cover influenced (≈ inverted benthos), and deep-sea distribution patterns in a single (OSPAR) region-based marine biogeographic approach.

In addition to aspects of other biogeographic approaches described in the chapters 5.2 ff., an integrated biogeographical approach has been elaborated. This approach integrates distribution patterns of different biocoenoses and taxa of both flora and fauna, as sessile and mobile organisms have extremely varied ecological requirements over the given geographical/oceanographical range and in a three-dimensioned space, also taking into account evolutionary and palaeoecologial aspects.

Temperature and to a lesser extent salinity are the most decisive factors to characterise water masses in their property to affect distribution patterns. But it is also important to take into account availability of food and changes in sediment structure, hydrostatic pressure, isotherms and thermoclines/pycnoclines, changes in light conditions, different currents in different water masses at different depths, alongslope and perpendicular turbidity currents on slopes, and disturbances in environment conditions. There are also other factors which together form complex patterns of vertical zonation and that are different in different latitudes, due to different water masses and the phenomenon of polar emergence and tropical submergence, and due to a different seasonality. Special features as seamounts, hydrothermal vents, cold seeps, cold water coral reefs/bioherms and the North East Water Polynya have been taken into account and discussed even though they are not biogeographic units of their own according to this classification.

In the deep-sea food (POM) is only available by a scarce allochtonuous input through surface – deep-sea coupling. A rare exception are those biocoenoses that rely on chemolithoautotrophic archaebacteria fuelled by sulphides or methane of hydrothermal vents and cold seeps. There is a biogeographic differentiation within the four known black and white smoker associations in the OSPAR area south of the Azores and even more pronounced differences from lower temperated hydrothermal locations in the northern seas. Biologic-functional correlations show that a real distinction of deep-sea (abyssal) faunal distributions from vertical migrating species and species with a high ecologic-vertical amplitude (Chap. 4.3) can be made only beyond depths with influence of light and input (*e.g.* of nutrients) from shelf areas (Chap. 6.1). Therefore, to get a number of practical and comparable units in spite of multiple isobathymetrical fringing belts and layers, the upper slopes of continental platforms, banks and islands (archibenthal depths of 200- ~1000 m) have been joined with shelf areas.

According to the requirements to get practical and useful units for nature protection purposes coming out of Annex V/Appendix 3 of the OSPAR convention this classification makes only one vertical division of the marine space and differentiates two deep-sea units (Arctic subregion, North Atlantic province) (Chap. 6.3.3; Fig. 107). This concept also reflects the phenomenon of polar emergence and tropical submergence of marine species, and applies to benthic and pelagic organisms.

Water temperature, fronts, and nutrients are the most decisive properties and factors for pelagic realms. Thus, the resulting subdivisions of the large scale water masses (holopelagial) are the ones which are superordinated to coastal neritic and benthic, Arctic ice influenced, and deep-sea entities. Dividing the water body of the OSPAR area into three entities:
(Holo)Pelagic biome (< 1000 m),
Benthal and **Neritopelagial** of the **Shelf** and **Upper Continental Slope** (< 1000 m), and **Ice-cover** biomes,
Deep-Sea biomes (Pelagial and Benthal > 1000 m),

further subdivisions have been identified and designated on different levels of a biogeographical hierarchy using the traditional systematic nomenclature where this exists (Chap. 6.4). Above the 1000 m isobath three pelagic provinces (Cold Arctic Waters, Cool-temperate Waters, Warm-temperate Waters) were defined (Chap. 6.3.1; Fig. 104). These function as higher units for the hierarchical differentiation of the "shallow" benthic, neritopelagic, and ice-cover influenced areas, thus leading to 18 subunits (11 provinces and 7 subprovinces) (Chap. 6.3.2; Figs. 104, 105).

In Arctic regions the role of ice related biocoenoses and ice-edge phytoplankton blooms as a base for arctic food webs is evident. On the other hand, the ice cover is limiting ordinary marine biotic patterns by reducing incoming radiation and thus by suppression of algal growth and above that by abrasion of sessile organisms at the littoral zone. High phytoplankton concentrations and an enhanced pelagic production are restricted to marginal ice zones and polynyas. Thus, ice-edges and polynyas, even though seasonally changing, are very significant for production in the high Arctic as well as for the composition and abundance of pelagic and benthic species. Therefore character and duration of ice cover *i.a.* acting as a substrate for biota and in addition fresh water influence combined with water depths/shelf-influence (benthic-pelagic coupling) serve as criteria for a differentiation and classification of Arctic provinces.

The designated "biological shelf" areas, unlike the geographical/topographical shelf of < 200 m depths, build one section together with the overlying neritopelagial waters and the ice cover (inverted benthal) in Arctic areas. Furthermore the different units are characterised by currents and water masses of a specific temperature regime and physio-oceanographical features as *e.g.* upwelling areas, ice-edges, and polynyas which shape biological distribution patterns.

The identified biogeographic units have been transferred into maps (Figs. 104, 105, 106, 107) and further presented, discussed, modified, and adopted at the OSPAR meetings at Oban/Scotland and Brest/France in 1999, and at the Isle of Vilm/Germany and Southampton/England in 2000 *i.a.* for the use within work for the OSPAR Annex V/Appendix 3 MPA-process.
Lower levels of biogeographical distinction are proposed to be identified on the level of meso-scale seascape-feature and community levels, macrobenthic community classifications, nutrient and productivity patterns, meso-scale fronts, eddies, mixing and stratification patterns, etc. above more differentiating habitat classifications (*e.g.* EUNIS).

10 Index of Figures

11 Bibliography

AAGAARD, K. (1981): On the circulation in the Arctic Ocean. – Deep-Sea Research 28: 251-268.

AAGAARD, K. & COACHMAN, L.K. (1968): The East Greenland Current north of Denmark Strait. – Arctic (21) part 1: 181-200; part 2: 267-290.

AAGAARD, K.; SWIFT, J.H. & CARMACK, E.C. (1985): Thermohaline circulation in the Arctic Mediterranean Seas. – Journal of Geophysical Research 90(C3): 4833-4846.

AAGAARD, K. & CARMACK, E.C. (1989): The role of sea ice and fresh water in the Arctic circulation. – Journal of Geophysical Research 94: 14485-14498.

ADAMS, J.A. (1982): Biological subdivisions of the North Sea. – In: OTTO, L. (Chairman) (Ed.): Flushing times in the North Sea. ICES Working group on flushing times for pollutants in the North Sea. ICES Cooperative Research Report 123.

AGARDY, M.T. (1994): Advances in marine conservation: the role of marine protected areas. – Trends in Ecology and Evolution (TREE) 9(7): 267-270.

ALEXANDER, L.M. (1992): Geographic Perspectives in the Management of Large Marine Ecosystems. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large marine ecosystems: patterns, processes and yields. – American Association for the Advancement of Science, Washington DC, USA.

ALEXANDER, V.A. (1992): Arctic Marine Ecosystems. – New Haven, Yale University, Connecticut.

ALVAREZ, M.; GALLARDO, T.; RIBERA, M.A. & GARRETA, A.G. (1988): A reassessment of northern Atlantic seaweed biogeography. – Phycologia 27: 221-233

AMBROSE, W.G. jr. & JUTERZENKA, K.v. (1994): Abundance, biomass, and spatial distribution pattern of brittle stars (Echinodermata: Ophiuroidea) on the Kolbeinsey Ridge north of Iceland. – Polar Biology 14: 185-194.

AMBROSE, W.G. jr. & RENAUD, P.E. (1995): Benthic response to water column productivity patterns: Evidence for benthic-pelagic coupling in the Northeast Water Polynya. – Journal of Geophysical Research 100(C3): 4411-4421.

AMBROSE, W.G. jr. & RENAUD, P.E. (1997): Does a pulsed food supply to the benthos affect polychaete recruitment patterns in the Northeast Water Polynya? – Journal of Marine Systems 10 (1-4): 483-495.

ANDREASEN, C. (1997): The prehistory of the coastal areas of Amdrup Land and Holm Land adjacent to the Northeast Water polynya: an archaeological perspective. – In: HIRCHE, H.-J. & DEMING, J.W. (Eds.): Northeast Water Polynya Symposium. – Journal of Marine Systems 10 (1-4): 41-46.

ANDREASEN, C. & LANGE, H. (1994): The Archaeology of Holm Land, Amdrup Land, and Henrik Krøyers Holme.– In: HIRCHE, H.-J. & KATTNER, G. (Eds.): The 1993 Northeast Water Expedition scientific cruise report of RV "Polarstern" Arctic cruises ARK IX/2 and 3, USCG "Polar Sea" cruise NEWP and the NEWLand expedition. – Berichte zur Polarforschung (142): pp 163-165.

ANGEL, M.V. (1977): Studies on Atlantic halocyprid ostracods: vertical distributions of the species in the top 1000m in the vicinity of 44°N 13°W. – Journal of the Marine Biological Association of the United Kingdom 57: 239-252.

ANGEL, M.V. (1979a): Studies on Atlantic halocyprid ostracods: their vertical distributions and community structure in the central gyre region along latitude 30° N off Africa and Bermuda. – Progress in Oceanography 8: 3-124.

ANGEL, M.V. (1979b): Zoogeography of the Atlantic Ocean. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.) (1979): Zoogeography and diversity of plankton. – (Arnold), London & (Bunge) Utrecht, pp 168-189.

ANGEL, M.V. (1982): Ocean trench conservation. – Commission on Ecology Papers No. 1. IUCN.

ANGEL, M.V. (1983): A vertical profile of planktonic ostracods at 42°N, 17°W from depths of 1500-3900m. pp 529-548 – In: MADDOCKS, R.F. (Ed): Applications of Ostracoda. – Geoscience Department, University of Houston, Texas.

ANGEL, M.V. (1984): The diel migrations and distributions within a mesopelagic community in the North East Atlantic. 3. Planktonic ostracods, a stable component in the community. – Progress in Oceanography 13: 319-351.

ANGEL, M.V. (1986): Vertical distribution: Study and implications.– In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO Technical Papers in Marine Science no. 49, Paris, pp 3-8.

ANGEL, M.V. (1991): Variations in time and space: is biogeography relevant to studies of long-time scale change. – Journal of the Marine Biological Association of the United Kingdom 71: 191-206.

ANGEL, M.V. (1993): Biodiversity of the pelagic oceans. – Conservation Biology 7: 760-762.

ANGEL, M.V. (1994): Spatial distribution of marine organisms: patterns and processes. – In: EDWARDS, P.J.R.; MAY, N.R. & WEBB, N.R. (Eds.): Large Scale Ecology and Conservation Biology. British Ecological Society Symposium No. 35. – (Blackwell Science) Oxford, pp 59-109.

ANGEL, M.V. (1997): Pelagic Biodiversity. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V.: Marine Biodiversity. Patterns and Processes. – Cambridge University Press, pp 35-68.

ANGEL, M.V. & BAKER, A. de C. (1982): Vertical distribution of the standing crop of plankton and micronekton at three stations in the Northeast Atlantic. – Biological Oceanography 2: 1-30.

ANGEL, M.V. & FASHAM, M.J.R. (1975): Analysis of the vertical and geographic distribution of the abundant species of planktonic ostracods in the North-east Atlantic. – Journal of the Marine Biological Association of the United Kingdom 55: 707-737.

ANGEL, M.V.; HARGRAEVES, P.; KIRKPATRICK, P. & DOMANSKI, P. (1982): Low variability in planktonic and micronektonic populations at 1000 m depth in the vicinity of 42° N, 17° W; evidence against diel migratory behaviour in the majority of species. – Biological Oceanography 1: 287-319.

ANGEL, M.V. & HARGRAEVES, P. (1992): Large scale patterns in the distribution of planktonic and micronektonic biomass in the northeast Atlantic. – ICES – Journal of Marine Science 49: 403-411.

ANKER-NILSSEN, T.; BARRETT, R.T. & KRASNOV, Y.V. (1996): Long-and short-term responses of seabirds in the Norwegian and Barents Sea to changes in stocks of prey fish. – In: Proceedings of the Role of Forage Fishes in Marine Ecosystems. Lowell Wakefield Fisheries Symp. – University of Alaska Sea Grant College Program, Report No. 97-01, pp 683-698.

AUEL, H. (1999): The Ecology of Arctic Deep-Sea Copepods (Euchaetidae and Aetideidae). Aspects of their Distribution, Trophodynamics and Effect on the Carbon Flux. – Berichte zur Polarforschung (319), 97 pp.

AUGIER, H. (1985): Les zones maritimes protégées. – Conseil de'l Europe, Strasbourg.

BACKUS, R.H. & CRADOCK, J.E. (1977a): Data report for Atlantic mesopelagic zoogeography. Woods Hole Oceanographic Institution, Technical Report-77-4: pp 1-8 (+ appendices).

BACKUS, R.H. & CRADOCK, J.E. (1977b): Pelagic faunal provinces and sounds-scattering levels in the Atlantic Ocean. – In: ANDERSON, N.R. & ZAHURANEC, B.J. (Eds.): Oceanic sound scattering prediction. – (Plenum Press) New York, London, pp 529-547.

BACKUS, R.H.; CRADOCK, J.E.; HAEDRICH, R.L. & ROBINSON, B.H. (1977): Atlantic Mesopelagic Zoogeography. – In: GIBBS, R.-H. jr. et al.: Fishes of the Western North Atlantic, No. 1, Memoir 1, Part 7 – Sears Foundation for Marine Research.Yale University, New Haven, pp 266-287.

BACKUS, R.H. (1986): Biogeographic Boundaries in the Open Ocean. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. Proceedings of an International Conference The Netherlands 29 May-5 June 1985. – UNESCO Technical Papers in Marine Science No. 49, Paris, pp 9-13.

BADCOCK, J. & MERRETT, N.R. (1977): On the distribution of Midwater Fishes in the Eastern North Atlantic. – In: ANDERSON, N.R. & ZAHURANEC, B.J. (Eds.): Oceanic sound scattering prediction. – (Plenum Press) New York, London, pp 249-282.

BAILEY, R.G. (1996): Ecosystem Geography. – (Springer) New York. 204 pp + maps.

BALYAEV, G.M.; VINOGRADOVA, N.G.; PASTERNAK, F.; SOKOLOVA, M.N. & FILATOVA, Z.A. (1973): Distribution patterns of deep-water bottom fauna related to the idea of the biological structure of the ocean. – Oceanology 13: 114-120 (English translation of Okeanologiya).

BĂNĂRESCU, P. & BOŞCAIU, N. (1978): Biogeographie. – (VEB Gustav Fischer Verlag), Jena.

BANKS, D.A. (1985): A fossil hydrothermal worm assemblage from the Tynagh lead-zinc deposit in Ireland. – Nature (London) 313: 128-131.

BANNER, F.T.; COLLINS, M.B. & MASSIE, K.S. (1980): The Northwest European shelf sea: the sea bed and the sea in motion. – (Elsevier) Amsterdam.

BARNES, R.S.K. & HUGHES, R.N. (1988): An Introduction to Marine Ecology. 2nd Ed. – (Blackwell Scientific Publications) Oxford, 351 pp.

BASFORD, D.; ELEFTHERIOU, A. & RAFFAELLI, D. (1990): The infauna and epifauna of the northern North Sea. – Netherlands Journal of Sea Research 25: 165-173.

BAUERFEIND, E.; GARRITY, C.; RAMSEIER, R. & WALSH, I. (1995): Variability of sediment trap collections as related to local sea-ice and oceanographic parameters. – NEW Symposium, Helsingør, Denmark, 1-5 May 1995.

BEARDALL, J.; FOSTER, P.; VOLTOLINA, D. & SAVIDGE, G. (1982): Observations on the surface water characteristics of the western Irish Sea. – Estuarine, Coastal and Shelf Science 14: 589-598.

BEARMAN, G. (Ed.) (1989): Ocean Circulation. 1. – The Open University. (Pergamon Press) Oxford. 238 pp.

BEGG, G.S. & REID, J.B. (1997): Spatial variation in seabird density at a shallow sea tidal mixing front in the Irish Sea. – ICES Journal of Marine Sciences 54: 552-565.

BEKLEMISHEV, C.W. (1969): Ecology and biogeography of the open ocean. – (Nauka) Moskow, pp 1-291 (in Russian).

BEKLEMISHEV, C.W. ; PARIN, N.V. & SEMINA, G.I (1977): Biogeography of the ocean. Pelagic zone. – In: VINOGRADOV, M.E. (Ed.): Oceanology. Biology of the ocean. (Nauka) Moskow, pp 219-261 (in Russian).

BELBIN, L. (1993): Environmental representativeness: regional partioning and reserve selection. – Biological Conservation 66: 223-230.

BELSKY, M.H. (1992): Interrelationship of Law in the Management of Large Marine Ecosystems. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large marine ecosystems: patterns, processes and yields. – American Association for the Advancement of Science, Washington DC, USA.

BENJAMINSEN, T. (1979): Pup production and sustainable yield of White Sea harp seals. – Fiskeridirektoratets (Norw.) Skrifter Ser. Havunters. 16: 551-559.

BERGER, W.H. (1974): Deep-Sea Sedimentation. – In: BURK, C.A. & DRAKE, C.L. (Eds.): The Geology of Continental Margins. (Springer) Berlin, pp 213-241.

BERGGREN, W.A. & HOLLISTER, C.D. (1977): Plate tectonics and paleocirculation – a commotion in the ocean. – Tectonophysics 38: 11-48.

BEUKEMA, J.J. (1992): Long-term and recent changes in the benthic macrofauna living on tidal flats in the western part of the Wadden Sea. – Netherlands Institute for Sea Research, Publication Series 20: 135-141.

BEVERTON, R.J.H. & A.J. LEE (1965): Hydrographic fluctuations in the North Atlantic Ocean and some biological consequences. – In: JOHNSON, C.G. & L.P. SMITH (Eds.): The biological significance of climate changes in Britain. – Institute of Biology Symposia, No. 14. (Academic Press) London, pp 79-107.

BILLET, D.S.M.; LAMPITT, R.S.; RICE, A.L. & MANTOURA, R.F.C. (1983): Seasonal sedimentation of phytoplankton to the deep-sea benthos. – Nature (London) 302: 520-522.

BIRD, C.F. & D. KELLETAT (1989): Zonality of Coastal Geomorphology and Ecology. Program, Abstracts and Field Guide. – Essener Geographische Arbeiten 18, 295 pp.

BLACKER, R.W. (1957): Benthic animals as indicators of hydrographic conditions and climatic change in Svalbard waters. – Fishery Investigations, London Ser. 2, 20(10): 1-49.

BLEAKLEY, C. & ALEXANDER, V. (1995): Marine Region 2, Arctic.– In: KELLEHER, G.; BLEAKLEY, C. & WELLS, S. (principal Eds.): A Global Representative System Of Marine Protected Areas, Vol. 1: Antarctic, Arctic, Mediterranean, Northwest Atlantic, Northeast Atlantic and Baltic. – Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN), pp 61-77.

BLINDHEIM, J. (1989): Ecological features of the Norwegian Sea. – In: REY, L. & ALEXANDER, V. (Eds.): Proceedings of the Sixth Conference of the Comité Arctique International, 13-15 May 1985, pp 366-401.

BLINDHEIM, J. (1990): Arctic intermediate water in the Norwegian Sea. – Deep-Sea Research 37: 1475-1489.

BLINDHEIM, J. & H. LOENG (1981): On the variability of Atlantic influence in the Norwegian and Barents Seas. – Fiskeridirektoratets Skrifter, Ser. Havunders. 17: 161-189.

BLINDHEIM, J. & SKJOLDAL, H.R. (1993): Effects of Climatic Change on the Biomass Yield of the Barents Sea, Norwegian Sea, and West Greenland Large Marine Ecosystems. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large Marine Ecosystems. Stress, Mitigation, and Sustainability. – AAAS. Washington DC, USA, pp 185-198.

BODE, A.; CASAS, B.; FERNÁNDEZ, E.; MARAÑÓN, E.; SERETT, P. & VARELA, M. (1996): Phytoplankton biomass and produktion in shelf waters off NW Spain: spatial and seasonal variability in relation to upwelling. – Hydrobiologia 341: 225-234.

BOEHLERT, G.W. & GENIN, A. (1987): A review of the effects of seamounts on biological processes. – In: KEATING, B.H.; FRYER, P.; BATIZA, R. & BOEHLERT, G.W. (Eds.): Seamounts, islands, and atolls. – Geophysical Monograph 43, American Geophysical Union, Washington DC, pp 319-334.

BOEHLERT, G.W. & MUNDY, B.C. (1993): Ichtyoplankton assemblages at seamounts and oceanic islands. – Bulletin of Marine Sciences 53(2): 336-361.

BØRGESEN, F. (1902): The marine Algae of the Faeröes. Reprint (1970) from Botany of the Faeröes, part II, Copenhagen 1903, and part III, London (1908). – (Linnaeus Press) Amsterdam. Also reprinted without change in paganation by (Det. Nordiske Forlag) Copenhagen.

BØRGESEN, F. (1908): The algae-vegetation of the Faeroese coasts with remarks on the phyto-geography.– In: WARMING, E. (Ed.): Botany of the Faeroes based upon Danish investigations. Part III, Appendix. – (John Weldon) London, pp 683-1070.

BØRGESEN , F. & JÓNSSON, H. (1905/1908): The distribution of the marine Algae of the Arctic and the northernmost Atlantic. – In: WARMING, E. (Ed.): Botany of the Faeroes based upon Danish investigations. Part III, Appendix. – (John Weldon) London, pp 1-28.

BORN,E.W.; WIIG, Ø. & THOMASSEN, J. (1997): *Seasonal and annual movements of radio-collared polar bears (Ursus maritimus) in northeast Greenland.* – In: HIRCHE, H.-J. & DEMING, J.W. (Eds.): Northeast Water Polynya Symposium. – Journal of Marine Systems 10 (1-4): 67-77.

BOLTOVSKOY, D. (1994): The sedimentary record of pelagic biogeography. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 135-160.

BOOTH, D.A. & ELLETT, D.J. (1983): The Scottish continental slope current. – Continental Shelf Research 2: 127-146.

BOTT, M.H.; SAXOV, S.; TALWANI, M. & THIE, J.H. (Eds.) (1983): Structure and development of the Greenland-Scotland ridge. – (Plenum Press) New York.

BOUCHET, P. & WARÉN, A. (1979): The abyssal molluscan fauna of the Norwegian Sea and its relation to other faunas. – Sarsia 64: 211-243.

BOURKE, R.H.; NEWTON, J.L.; PAQUETTE, P.G. & TUNNICLIFFE, M.D. (1987): Circulation and Water masses of the East Greenland Shelf. – Journal of Geophysical Research 92(C7): 6729-6740.

BOWEN, R. (1966): Paleotemperature analysis. – (Elsevier) New York, 265 pp.

BRADSTREET, M.S.W. & CROSS, W.E. (1982): Trophic relationships at High Arctic ice edges. – Arctic 35: 1-12.

BRADSTREET, M.S.W. (1988): Importance of ice edges to High Arctic seabirds. – In: OULETTE, H. (Ed.): Proceedings of the XIX International Congress Ottawa. – (University of Toronto Press) Toronto, pp 997-1000.

BRAMWELL, M. (Ed.) (1977): The atlas of the oceans. – (Mitchell Beazley Publishers) London, UK.

BRANDT, A. (1993): Composition, abundance and diversity of peracarid crustaceans on a transect of the Kolbeinsey Ridge, north of Iceland. – Polar Biology 13: 565-576.

BRANDT, A. (1995) : Peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya off Greenland: documenting close benthic-pelagic coupling in the Westwind Trough. – Marine Ecology Progress Series 121: 39-51.

BRANDT, A. & PIEPENBURG, D. (1994): Peracarid crustacean assemblages of the Kolbeinsey Ridge, north of Iceland. – Polar Biology 14: 97-105.

BRANDT, A.; SVAVARSSON, J. & BRATTEGARD, T. (1994): *Eurycope brevirostris* (Isopoda; Asellota) from the deep Arctic Ocean; redescription, postmarsupial development, and reproductive patterns. – Sarsia 79: 127-143.

BRANDT, A.; VASSILENKO, S.; PIEPENBURG, D. & THURSTON, M. (1996): The species composition of the peracarid fauna (Crustacea, Malacostraca) of the Northeast Water Polynya (Greenland). – Meddelelser om Grønland. – Bioscience 44: 1-30.

BRATTEGARD, T. & HOLTHE, T. (1995): Kartlegging av egnede marine verneområder i Norge. – Tilrådning fra rådgivende utvalg. Utredning for DN Nr. 1995-3, Avgitt til Direktoratet for Naturforvaltning, Trondheim. 174 pp.

BRATTEGARD, T. & HOLTHE, T. (1997): Distribution of marine, benthic macro-organisms in Norway. A tabulated catalogue. Preliminary edition. – Utredning/Research Report for DN Nr. 1997-1. Direktoratet for Naturforvaltning, Trondheim. 409 pp.

BRATTSTRÖM, H. (1977): Marin zoogeography. Kompendium. – Institut for Marinbiologi, Universitetet i Bergen, 128 pp.

BREEMANN, A.M. (1988): Factors that keep seaweeds within their geographic boundaries: experimental and phenological evidence. – Helgoländer Meeresuntersuchungen 42: 199-241, Hamburg.

BRIGGS, J.C. (1966): Oceanic islands, endemism and marine paleotemperatures. – Systematic Zoology 15: 153-163.

BRIGGS, J.C. (1970): A faunal history of the North Atlantic Ocean. – Systematic Zoology 19: 19-34.

BRIGGS, J.C. (1974): Marine Zoogeography. – (McGraw-Hill Book Co.) New York, USA, 475 pp.

BRIGGS, J.C. (1984): Centres of origin in biogeography. – Biogeographical Monograph No. 1, University of Leeds, Leeds.

BRIGGS, J.C. (1987): Biogeography and Plate Tectonics. – Developments in Palaeontology and Stratigraphy 10. (Elsevier) Amsterdam, 204 pp.

BRIGGS, J.C. (1994): Species diversity: land and sea compared. – Systematic Zoology 43: 130-135.

BRIGGS, J.C. (1995): Global Biogeography. – Developments in Palaeontology and Stratigraphy 14. (Elsevier) Amsterdam, 452 pp.

BROEKER, W.S. & DENTON, G.H. (1989): The role of ocean-atmosphere reorganizations in glacial cycles. – Geochimica et Cosmochimica Acta 53: 2465-2501.

BROWN, R.G.B. & NETTLESHIP, D.N. (1981): The biological significance of polynyas to arctic colonial seabirds.– In: STIRLING, I. & CLEATOR, H. (Eds.): Polynyas in the Canadian Arctic. – Canadian Wildlife Service Occasional Paper 45, Ottawa, pp 59-65.

BRUUN, A.F. (1956): The abyssal fauna: Its ecology, distribution and origin. – Nature (London) 177: 1105-1108.

BRUUN, A. (1957): Deep-sea and abyssal depth.– In: HEDGEPETH, J.W. (Ed.): Treatise on marine ecology and paleoecology. – Geological Society of America, Memoir 67, Vol. 1: 641-672.

BUBNOV, V.A. (1968): Boundaries of intermediate water masses in the North Atlantic. – Oceanology, Vol. 8: 322-325.

BURK, C.A. & DRAKE, C.L. (1974): The geology of continental margins. – (Springer-Verlag) New York 1,009 pp.

CABIOCH, L. (1968): Contribution a la connaissance des peuplements benthiques de la Manche occidentale. – Cahiers de Biologie Marine (Supplements) 9: 493-720.

CABIOCH, L.; GENTIL, F.; GLAÇON, R. & RETIÈRE, C. (1977): Le macrobenthos des fonds meubles de la Manche: distribution générale et écologie.– In: KEEGAN, B.F.; CEIDIGH, P.Ó. & BOADEN, P.J.S. (Eds.): Biology of Benthic Organisms. – 11th European Symposium on Marine Biology, Galway, October 1976. – (Pergamon Press) New York, Oxford, pp 115-128.

CAMBRIDGE, M.; BREEMANN, A.M. & VAN DEN HOEK, C. (1984): Temperature responses of some North Atlantic Cladophora species (Chlorophyceae) in relation to their geographic distribution. – Helgoländer Meeresuntersuchungen 38: 349-363.

CAREY, A.G. (1985): Marine Ice Fauna: Arctic. – In: HORNER, R.A. (Ed.): Sea Ice Biota. – (CRC Press) Boca Raton, Florida, pp 173-190.

CARNEY, R.S.; HAEDRICH, R.L. & ROWE, G.T. (1983): Zonation of Fauna in the Deep Sea. – In: ROWE, G.T. (Ed.): Deep-Sea Biology. The Sea, Vol. 8. (John Wiley and Sons) New York, pp 453-472.

CASANOVA, J.P. (1977): La faune pélagique profonde (zooplancton et necton) de la province atlanto-méditerranéenne. Aspects taxonomique, biologique et zoogéographique. – (Thèse Doctorat Etat-Sciences Naturelle) Université de Provence, Aix-Marseille: 1-455.

CHANG-TAI SHIH (1979): East-West diversity.– In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.) (1979): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge), Utrecht, pp 87-102.
CHASSÉ, C. & GLÉMAREC, M. (1976): Atlas des fond meubles du plateau continental du Golfe de Gascogne. – (Imprimerie ICA) Brest.
CHEVALDONNÉ, P. (1997): The fauna of deep-sea hydrothermal vents, an introduction. – In: DESBRUYÈRES, D. & SEGONZAC, M. (Eds.): Handbook of deep-sea hydrothermal vent fauna. – (Éditions IFREMER) Brest, France, pp 7-10.
CHRISTIANSEN, M.E. (1982): A review of the distribution of Crustacea Decapoda Brachyura in the Northeast Atlantic. – Quaderni del Laboratorio di Technologia della Pesca 3: 347-354.
CHURKIN, M. JR. & TREXLER, J.H. jr. (1981): Arctic Continental Plates and Accreted Oceanic Terranes. – In: NAIRN, A.E.M.; CHURKIN, M. & STELHI, F.G. (Eds.): The ocean basins and margins. Vol. 5: The Arctic Ocean. (Plenum Press) New York, pp 1-20.
CLARK, D.L. (1971): Arctic ocean ice cover and its late Cenozoic history. – Geological Society of America Bulletin 82: 3314-3324.
CLARK, D.L. (1975): Geological history of the Arctic Ocean Basin. – In: YORATH, C.J.; PARKER, E.R. & GLASS, D.J. (Eds.): Canada's continental margins. – Canadian Society of Petroleum Geologists, Calgary, pp 501-524.
CLARKE, A.H. jr. (1962): On the composition, zoogeography, origin and age of the deep-sea mollusk fauna. – Deep-Sea Research 9: 291-306.
CLARKE, A. (1992): Is there a latitudinal diversity in the Sea? – Trends in Ecology and Evolution 7: 286-287.
CLARKE, A. & CRAME, A. (1997): Diversity, latitude and time: Patterns in the shallow sea. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V. (EDS.): Marine Biodiversity. Patterns and Processes. (Cambridge University Press), Cambridge, pp 122-147.
CLOUGH, L.M.; AMBROSE, W.G. JR.; ASHJIAN, C.J.; PIEPENBURG, D.; RENAUD, P.E. & SMITH, S.L. (1997): Meroplankton abundance in the Northeast Water Polynya: Insights from oceanographic parameters and benthic abundance patterns. – Journal of Marine Systems 10(1-4): 343-357.
COACHMAN, L.K. & AAGAARD, K. (1974): Physical Oceanography of Arctic and Subarctic Seas. – In: HERMAN, Y. (Ed.): Marine Geology and Oceanography of the Arctic Seas. (Springer) Berlin, pp 1-72.
COLEBROOK, J.M. (1964): Continuous plankton records: A principal components analysis of the geographical distribution of zooplankton. – Bulletin of Marine Ecology 6: 78-100.
COLEBROOK, J.M. (1978): Continuous Plankton Records: zooplankton and environment, north-east Atlantic and North Sea, 1948-1975. – Oceanologica Acta 1: 9-23.
COMMISSION OF THE EUROPEAN COMMUNITIES, DG11 (1991): Corine biotopes manual – Habitats of the European Community, Data specifications part 2., Luxembourg.
CONNOR, D.W. (1991): Norwegian fjords and Scottish sea lochs: a comparative study. – Joint Nature Conservation Commitee Report, No. 12 (Marine Nature Conservation Review Report, No. MNCR/SR/18).
CONNOR, D.W.; HISCOCK, K.; FOSTER-SMITH, R.L. & COVEY, R. (1995): A classification system for benthic marine biotopes. – In: ELEFTHERIOU, A.; ANSELL, A.D. & SMITH, C.J. (Eds.): Biology and ecology of shallow coastal waters. Proceedings of the 28th European Marine Biology Symposium. (Publ. Friedensborg, Olsen and Olsen), pp 155-165.
CONNOR, D.W.; BRAZIER, D.P.; HILL, T.O.& NORTHEN, K.O. (1997): Marine Nature Conservation Review: Marine biotope classification for Britain and Ireland, Vol. 1: Littoral biotopes: Version 97.06, – JNCC Report No. 229.
CONNOR, D.W.; DALKIN, M.J.; HILL, T.O.; HOLT, R.H.F. & SANDERSON, W.G. (1997): Marine Nature Conservation Review: Marine biotope classification for Britain and Ireland, Vol. 2: Sublittoral biotopes: Version 97.06, – JNCC Report No. 230.
CONOVER, R.J. (1979): Secondary production as an ecological phenomenon. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.) (1979): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 50-86.
COUPER, A. (Ed.) (1989): Atlas and Encyclopaedia of the Sea. – (Times Books Ltd.), London.

COSTELLO, M.J.; EMBLOW, C.S. & PICTON, B.E. (1996): Long term trends in the discovery of marine species new to science which occur in Britain and Ireland. – Journal of the Marine Biological Association of the United Kingdom 76: 255-257.

COX, C.B.M.; I.N. HEALEY & P.D. MOORE (1973): Biogeography. An ecological and evolutionary approach. – (Blackwell) Oxford, 179 pp.

COX, C.B. & MOORE, P.D. (2000): Biogeography. An ecological and evolutionary approach. (6th edn.) – (Blackwell Science) Oxford, 298 pp.

CRAME, J.A. (1991): An evolutionary framework for the polar regions. – Journal of Biogeography 24: 1-9.

CRANE, K. & J.J. GALASSO (1999): Arctic environmental atlas. – Office of Naval Research, Naval Research Laboratory, Hunter College, Washington, DC, 164 pp.

CRISP, D.J. (1958): The spread of *Elminius modestus* Darwin in north-west Europe. – Journal of the Marine Biological Association of the United Kingdom, 37: 483-520.

CRISP, D.J. (1989): The influence of tidal fronts on the distribution of intertidal fauna and flora. – In: ROS, J.D.: Topics in marine biology. 22nd European Marine Biology Symposium. – Scientia Marina 53: 283-292

CRISP, D.J. & FISCHER-PIETTE, É. (1959): Répartition de principales espèces intercotidales de la côte Atlantique française en 1954-55. – Annales de l'Institute Océanographique, Monaco 36(2): 275-388.

CRISP, D.J. & KNIGHT-JONES, E.W. (1955): Discontinuities in the distribution of shore animals in north Wales. – Report of Bardsey Bird and Field Observatory 2: 29-34.

CRISP, D.J. & A.J. SOUTHWARD (1953): Isolation of intertidal animals by sea barriers. – Nature (London) 172: 208.

CRISP, D.J. & SOUTHWARD, A.J. (1958): The distribution of intertidal organisms along the coast of the English Channel. – Journal of the Marine Biological Association of the United Kingdom 37: 157-208.

CROWLEY, T.J. (1981): Temperature and circulation changes in the eastern North Atlantic during the last 150,000 years: evidence from the planktonic foraminiferal record. – Marine Micropaleontology 6: 97-129, Amsterdam.

CURTIS, M.A. (1973): The marine benthos of Arctic and Subarctic continental shelves. – Polar Record 17(111): 595-626.

CUTLER, E.B. & CUTLER, N.J. (1987): Deep-water Sipuncula from the eastern Atlantic Ocean. – Sarsia 72: 71-89.

DAHL, E. (1972): The Norwegian Sea deep-water fauna and its derivation. – Ambio Special Report 2: 19-24.

DAHL, E. (1979): Amphipoda Gammaridea from the deep Norwegian Sea. A preliminary report. – Sarsia 64(1-2): 57-59.

DAHL, E.; LAUBIER, L.; SIBUET, M. & STRÖMBERG, J.-O. (1979): Some quantitative results on benthic communities of the deep Norwegian Sea. – Astarte 9: 61-79.

DARBY, M.S.; WILLMOTT, A.J. & SOMERVILLE, T.A. (1995): On the influence of coastline orientation on the steady state width of a latent heat polynya. – Journal of Geophysical Research 100: 13625

DARWIN, C. (1859): The origin of species by means of natural selection. – (John Murray) London.

DAUVIN, J.-C.; BELLAN, G.; BELLAN-SANTINI, D.; CASTRIC, A.; COMOLET-TIRMAN, J.; FRANCOUR, P.; GENTIL, F.; GIRARD, A.; GOFAS, S.; MAHÉ, C.; NOËL, P. & DE REVIERS, B. (1994): Typologie des ZNIEFF-mer. Liste des paramètres et des biocœnoses des côtes françaises métropolitaines. 2éme Édition. – Collection Patrimoines Naturels. Série Patrimoines écologique. Secrétariat de la Faune et la Flore, Muséum National d'Histoire Naturelle 12, Paris, 70pp.

DAUVIN, J. -C. (Ed.) (1997): Les biocénoses marines et littorales françaises des côtes Atlantiques, Manche et Mer du Nord; synthèse, menaces et perspectives. – Laboratoire de Biologie et Invertébrés Marine et Malacologie – Service du Patrimoines Naturel/IEGB/MNHN, Paris, 376 pp.

DAVY DE VIRVILLE, A. (1940): Les zones de végétation sur le littoral atlantique. – Mémoires de la Société de Biogéographie, Paris 7: 205-251.

DAWES, P.R. & PEEL, J.S. (1981): The Northern Margin of Greenland from Baffin Bay to the Greenland Sea. – In: NAIRN, A.E.M.; CHURKIN, M. & STELHI, F.G. (Eds.): The ocean basins and margins. Vol. 5: The Arctic Ocean. – (Plenum Press) New York & London, pp 201-264.

DAY, J. & ROFF, J. (1999): Planning for Representative Marine Protected Areas: A Framework for Canada's Oceans. – ed. by LAUGHREN, J. & LAVOIE, K., WWF Canada, Toronto.

DAYTON, P.K. & HESSLER, R.R. (1972): Role of biological disturbance in maintaining diversity in the deep sea. – Deep-Sea Research 19: 199-208.

DE LATTIN, G. (1967): Grundriss der Zoogeographie. – (VEB Gustav Fischer Verlag) Jena, 602 pp.

DEMING, J.; GAYLORD, J.; CARPENTER, S. & MAPLES, C. (1995): Benthic bacterial activity in the NEW Polynya – Summers 1992 and 1993. – NEW Symposium, Helsingør, Denmark, 1-5 May 1995.

DE MOL, B. (Ed.) (1998): Geosphere-Biosphere Coupling: Carbonate Mud Mounds and Cold Water Reefs. – Intergovernmental Oceanographic Commission, Workshop Report No. 143.

DEN HARTOG, C. (1970): The Sea-grasses of the world. – (North-Holland Publishers) Amsterdam, 275 pp.

DESBRUYÈRES, D. & SEGONZAC M. (Eds.) (1997): Handbook of deep-sea hydrothermal vent fauna. – (Éditions IFREMER) Brest, France, 279 pp.

DEVILLIERS, P. & DEVILLIERS-TERSCHUREN, J. (1996): A classification of Palaearctic habitats. – Nature and Environment, No. 78, (Council of Europe Publishing) Strasbourg.

DICKEY-COLLAS M.; GOWEN, R.J. & FOX, C.J. (1996): Distribution of Larval and Juvenile Fish in the Western Irish Sea: Relationship to Phytoplankton, Zooplankton Biomass and Recurrent Physical Features. – Marine and Freshwater Research 47: 169-81.

DICKSON, R.R.; MEINCKE, J.; MALMBERG, S.-A. & LEE, A.J. (1988): The "great salinity anomaly" in the Northern North Atlantic. – Progress in Oceanography 20: 103-151.

DIETRICH, G. (1963): General oceanography: an introduction. – (John Wiley Interscience Publishers) New York, 588 pp.

DIETRICH, G. (1964): Oceanic polar front survey in the North Atlantic. Research in Geophysics 2. – In: ODISHAW, H. (Ed.): Solid earth and interface phenomena. – (M.I.T. Press) Cambridge, Mass., USA, pp 291-308.

DIETRICH, G. (1970): Ozeanographie. – (Westermann) Braunschweig, 118 pp.

DIETRICH, G.; KALLE, K. & SIEDLER, G. (1975): Allgemeine Meereskunde. 3. Aufl. – (Gebrüder Bornträger) Berlin, Stuttgart, 593 pp.

DINTER, W.P. (1998): Biogeographische Einheiten der Meeresgebiete im Bereich der OSPAR-Konvention. – Bundesamt für Naturschutz, Isle of Vilm, Germany. 99 pp + maps (in German with English abstract, unpublished).

DINTER, W.P. (1999): Biogeographical units of the OSPAR Maritime Area. – Papers presented on the OSPAR/ICES/EEA Workshop on Habitat Classification and Biogeographic regions, Oban/Scotland, 6.-10.9.1999.

DINTER, W.P. (2000a): Biogeography of the North-East Atlantic. – Papers presented on the 2nd Workshop on Marine Protected Areas in the OSPAR area. Bundesamt für Naturschutz (Federal Agency for Nature Conservation), Isle of Vilm/Germany, 5.-9.6.2000.

DINTER, W.P. (2000b): Biogeography of the OSPAR Maritime Area. – Papers presented on the 2nd OSPAR/ICES/EEA Workshop on Habitat Classification, Southampton/England, 18-22.9.2000.

DIXON, P.S. (1965): Changing patterns of distribution in marine algae. – In: JOHNSON, C.G. & SMITH, L.P. (Eds.): The biological significance of climate changes in Britain. – Institute of Biology Symposia, No. 14. – (Academic Press) London, pp 109-115.

DIVOKY, G.J. (1977): Sea ice as factor in seabird distribution and ecology in the Beaufort, Chukchi and Bering Seas. – In: BARTONEK, J.C. & NETTLESHIP, D.N. (EDS.): Conservation of marine birds of northern North America. – Washington, D.C.: U.S. Fish and Wildlife Service, Wildlife Research, Departmend 11, pp 9-19.

DOMANSKI, P.A. (1986): The Azores front: A zoogeographic boundary? – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an International Conference The Netherlands 29 May-5 June 1985. – UNESCO Technical Papers in Marine Science No. 49, Paris, pp 73-83.

DRAGESUND, O. & GJØSÆTER, J. (1988): The Barents Sea. – In: POSTMA, H. & ZIJLSTRA, J.J. (Eds.): The ecosystems of the world. Vol. 27. Continental shelves. – (Elsevier) Amsterdam, pp 339-361.

DUNBAR, M.J. (1951): Eastern Arctic Waters. – Bulletin of the Fisheries Research Board of Canada 88: 131

DUNBAR, M.J. (1953): Arctic and Subarctic marine ecology. – Arctic 6(2): 75-90.
DUNBAR, M.J. (1955): Water masses, circulation, ice cover. – In: KIMBLE, G.H.T. & GOOD, D. (Eds.): Geography of the Northlands. – American Geographical Society, New York, and (John Wiley & Sons) New York, pp 36-57.
DUNBAR, M.J. (Ed.) (1963): Marine distributions. – Toronto (University Press) – Special Publications of the Royal Society of Canada, Vol. 5., pp 3-8.
DUNBAR, M.J. (1968): Ecological development in Polar Regions. – (Prentice-Hall) New Jersey, 119 pp.
DUNBAR, M.J. (1972): The nature and definition of the marine Subarctic, with a note on the sea-life of the Atlantic Salmon. – Transactions of the Royal Society of Canada 10: 249-257.
DUNBAR, M.J. (Ed.) (1977 a): Polar Oceans. – Arctic Institute of North America, Calgary, Canada.
DUNBAR, M.J. (Ed.) (1977 b): The evolution of polar ecosystems. – In: LLANO, G.A.: Adaptions within Antarctic ecosystems. Smithsonian Institution, Washington, DC, pp 1063-1076.
DUNBAR, M.J. (1979): The relation between oceans. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 112-125.
DUNBAR, M.J. (1981): Physical causes and biological significance of polynyas and open water in sea ice. – In: STIRLING, I. & CLEATOR, H. (Eds.): Polynyas in the Canadian Arctic. – Canadian Wildlife Service Occasional Paper 45, Ottawa, pp 29-43.
DUNBAR, M.J. (1982): Arctic marine Ecosystems. – In: REY, L. & STONEHOUSE, B. (Ed.): The Arctic Ocean. The hydrographic environment and the fate of pollutants. – (Macmillan Press Ltd.) London, UK.
DUNBAR, M.J. (1985): The Arctic Marine Ecosystem. – In: ENGELHARDT, F.R. (Ed.): Petroleum Effects in the Arctic Environment. – (Elsevier Applied Science Publishers) London and New York, pp 1-35.
DUNTON, K. (1992): Arctic biogeography: The paradox of the marine benthic fauna and flora. – Trends in Ecology and Evolution (TREE) Vol. 7, No. 6: 183-189.
EARLL, R. & ERWIN, D.G. (Eds.) (1983): Sublitoral Ecology. The ecology of the shallow sublittoral benthos. – (Clarendon Press) Oxford, 277 pp.
EARLL, R. & FARNHAM, W. (1983): Biogeography. – In: EARLL, R. & ERWIN, D.G. (Eds.) Sublitoral Ecology. The ecology of the shallow sublittoral benthos. – (Clarendon Press) Oxford, pp 165-208.
EBELING, A.W. (1967): Zoogeography of tropical deep-sea animals. – Studies in Tropical Oceanography 5: 593-613.
EINSELE, G. (1992): Sedimentary Basins. – (Springer) Berlin, Heidelberg.
EKMAN, S. (1935): Tiergeographie des Meeres. – (Akademische Verlagsgesellschaft) Leipzig.
EKMAN, S. (1953): Zoogeography of the Sea. – (Sidgwick & Jackson Ltd.) London, 417 pp.
ELDER, D. & PERNETTA, J. (1991): Oceans. – (IUCN & Mitchell Beazley Publishers) London.
ELLETT, D.J.; EDELSTEN, D.J. & BOOTH, D.A. (1980): Measurement of a continental slope current west of Scottland. – International Council for the Exploration of the Sea (C.M. Papers and Reports) C 8, 5 pp.
ELLIS, C.J. (1985): The effects of proximity to the continental slope sea-bed on pelagic halocyprid ostracods in the northeast Atlantic Ocean at 49°N, 13°W. – Journal of the Marine Biological Association of the United Kingdom 65(4): 923-949.
ELLIS, D.V. & WILCE, R.T. (1961): Arctic and subarctic examples of intertidal zonation. – Arctic 14: 224-235.
ELLIS, J.R.; ROGERS, S.I. & FREEMAN, S.M. (2000): Habitat Complexes in the offshore waters of the British Isles. – Discussion Document for the 2nd OSPAR/ICES/EEA Workshop on Habitat Classification, Southampton/England, 18-22.9.2000.
ELLIS, J.R.; ROGERS, S.I. & FREEMAN, S.M. (2000): Demersal assemblages in the Irish Sea, St. George's Channel and Bristol Channel. – Estuarine, Coastal and Shelf Science Vol. 51, No. 3: 299-315.
ENO, N.C.; CLARK, R.A. & SANDERSON, W.G. (Eds.) (2000): Directory of non-native marine species in British waters. – http://www.jncc.gov.uk/marine dns/ .
EPP, D. & SMOOT, N.C. (1989): Distributions of seamounts in the North Atlantic. – Nature (London) 337: 254-257.
ESCOBAR-BRIONES, E.; ROWE, G.; BOLAND, G. & NEWTON, A. (1995): Sediment oxygen demand in the Northeast Water Polynya, Greenland. – NEW Symposium, Helsingør, Denmark, 1-5 May 1995.

ETTER, R.J. & GRASSLE, F.J. (1992): Patterns of species diversity in the deep sea as a function of sediment particle size diversity. – Nature (London) 360: 576-578.

EVANS, R.G. (1957): The intertidal ecology of some localities on the Atlantic coast of France. – Journal of Ecology 45: 245-271.

FAIRBRIDGE, R.W. (Ed.) (1966): Oceans, limits definition and dimension. – In: Encyclopedia of Earth Science Series, Encyclopedia of Oceanography, Vol. 1. (Reinhold Publishing Corp.) New York, NY, USA, pp 632-640.

FALK, K. & MØLLER, S. (1995): Colonies of Northern Fulmars and Black-legged Kittiwakes associated with the Northeast Water Polynya Northeast Greenland. – Arctic Vol. 48, No. 2: 186-195.

FALK, K.; HJORT, C.; ANDREASEN, C.; CHRISTENSEN, K.D.; ELANDER, M.; ERICSON, M.; KAMPP, K.; KRISTENSEN, R.M.; MØBJERG, N.; MØLLER, S. & WESLAWSKI, J.M. (1997): *Seabirds utilizing the Northeast Water polynya.* – In: HIRCHE, H.-J. & DEMING, J.W. (Eds.): Northeast Water Polynya Symposium. – Journal of Marine Systems 10 (1-4): 47-65.

FAO/FOOD AND AGRICULTURE ORGANIZATION (1972): Atlas of the living resources of the sea. – FAO, Rome.

FARNHAM, W.F. (1980): Studies on aliens in the marine flora of southern England. – In: PRICE, J.H.; IRVINE, D.E.G. & FARNHAM, W.F. (Eds.): The shore environment, Vol. 2: Ecosystems. – Systematics Association Special Volume, No. 17B, (Academic Press) London, pp 875-914.

FASHAM, M.J.R. & ANGEL M.V. (1975): The relationship of the zoogeographic distribution of the planktonic ostracods in the North-East Atlantic to the water masses. Journal of the Marine Biological Association of the United Kingdom 55(3): 739-757.

FASHAM, M.J.R. & FOXTON, P. (1979): Zonal distribution of pelagic decapoda (Crustacea) in the eastern North Atlantic and its relation to the physical oceanography. – Journal of Experimental Marine Biology and Ecology 37: 225-253.

FASHAM, M.J.R.; PLATT, T.; IRWIN, B. & JONES, K. (1985): Factors affecting the spatial pattern of the deep chlorophyll maxima in the region of the Azores Front. – Progress in Oceanography 14: 129-166.

FAUVEL, P. (1959): Classe des annélides polychètes. Distribution géographique. – Traité de Zoologie 5(1): 163-165.

FISCHER, P.-H. (1943): Mollusques marins des Archipels atlantiques. Considérations sur la biogéographie littorale de l'Atlantique Nord. – Comtes Rendu Sommaire des Séances de la Société de Biogéographie: pp 4-7.

FISCHER-PIETTE, É. (1935): Quelque remarques bionomiques sur la côte basque française et espagnole. – Bulletin du Laboratoire maritime du Muséum d'Histoire naturelle de Saint-Servan 14: 1-14.

FISCHER-PIETTE, É. (1936): Études sur la biogéographie intercotidale des deux rives de la Manche. – The journal of the Linnean Society of London, Zoology, Vol. 40, No. 270: 181-272.

FISCHER-PIETTE, É. (1938): Sur le caractère méridional du bios intercotidal du golfe de Gascogne. – Comtes Rendu Sommaire des Séances de la Société de Biogéographie, 15: 61-65.

FISCHER-PIETTE, É. (1952): La distribution des Fucacées sur la côte Nord d'Espagne en 1949. – Bulletin du Laboratoire maritime de Dinard, fascicule 37: p 1-13.

FISCHER-PIETTE, É. (1953): Répartition de quelques Mollusques intercotideaux communs le long des côtes septentrionales de l'Espagne. – Journal de Conchyliologie XCIII: 39-73.

FISCHER-PIETTE, É. (1955): Répartition, le long des côtes septentrionales de l'Espagne, des principales espèces peuplant les rochers intercotideaux. – Annales de l'Institut Océanographique, Monaco 31(2): 37-124.

FISCHER-PIETTE, É. (1957): Sur des déplacements des frontières biogéographiques observés au long des côtes ibériques dans le domaine intercotidal. – Simposio de Biogeographia Ibérica. – Publicaciones del Instituto de Biologia Aplicada 26 : 35-40.

FISCHER-PIETTE, É. (1963): La distribution des principeaux organismes intercotidaux Nord-Ibériqueens 1954-1955. – Annales de l'Institut Océanographique, Monaco 40(3): 165-312.

FISCHER-PIETTE, É. & PRENANT, M. (1956): Distribution des cirripèdes intercotidaux d'Espagne septentrionale. – Bulletin du Centre d'Etudes et de Recherches Scientifiques de Biarritz 1(7): 67-90.

FIÚZA, A.F.G. (1983): Upwelling patterns off Portugal. – In: SUESS, E. & THIEDE, J. (Eds.): Coastal Upwelling, Its sedimentary record. – NATO Conference Series 4, Part A: Responses of the

Sedimentary Regime to Present Coastal Upwelling. Marine Sciences 10, (Plenum Press) New York, pp 85-98.

FIÚZA, A.F.; DE MACEDO, M.E. & GUERREIRO, M.R. (1982): Climatological space and time variation of the Portuguese coastal upwelling. – Oceanologica Acta 5: 31-40.

FLACH, E. & THOMSEN, L. (1998): Do physical and chemical factors structure the macrobenthic community at the continental slope in the NE Atlantic? – Hydrobiologia 375/376: 265-285.

FLATO, G.M. (1995): Spatial and temporal variability of Arctic ice thickness. – Annals of Glaciology 21: 323-329

FLEMINGER, A. & HULSEMANN, K. (1977): Geographical range and taxonomic divergence in the North Atlantic Calanus (*C.helgolandicus*, *C. finnmarchicus* and *C. glacialis*). – Marine Biology 40: 233-248.

FORBES, E. (1856): Map of the distribution of marine life. Plate No. 31 – In: JOHNSTON, A.K.: The physical atlas of natural phenomena (new edition). (W. and A.K. Johnston) Edinburgh and London. (1st edit. 1854).

FORBES, E. & GODWIN-AUSTEN, R. (1859): The Natural History of the European Seas. – (Van Voorst) London, 306 pp.; Reprint (1977): (Arno Press) New York.

FOXTON, P. (1972): Observations on the vertical distribution of the genus Acanthephyra (Crustacea: Decapoda) in the eastern North Atlantic, with particular reference to the "purpurea" group. – Proceedings of the Royal Society of Edinburgh B 73: 301-313.

FRAGA, F. (1981): Upwelling off the Galician coast, Northwest Spain. – In: RICHARDS, F.W. (Ed.): Coastal Upwelling. – American Geophysical Union, pp 176-182.

FRANCE, R. & SHARP, M. (1992): Polynyas as centers of organization for structuring the integrity of Arctic marine communities. – Conservation Biology. 6(3): 442

FRANEKER, J.A. VAN & WATTEL, J. (1982): Geographical variation of the Fulmar (*Fulmarus glacialis*) in the North Atlantic. – Ardea 70: 31-44.

FRASER, J.H. (1968): The overflow of oceanic plankton to the shelf-waters of the North-east Atlantic. – Sarsia 34: 313-330.

FREDERIKSEN, R.; JENSEN, A. & WESTERBERG, H. (1992): The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe Islands and the relation to internal tidal mixing. – Sarsia 77: 157-171.

FREIWALD, A. (1998): Geobiology of *Lophelia pertusa* (Scleractinia) reefs in the North Atlantic. – Habilitationsschrift (Fachbereich Geowissenschaften) Universität Bremen, 116 pp.

FRICKE, H.; GIERE, O.; STETTER, K.; ALFREDSSON, G.A.; KRISTJANSSON, J.K.; STOFFERS, P. & SVAVARSSON, J. (1989): Hydrothermal vent communities at the shallow subpolar Mid-Atlantic ridge. – Marine Biology 102: 425-429.

FRIEDRICH, C. (1997): Ökologische Untersuchungen zur Fauna des arktischen Meereises. – Berichte zur Polarforschung 225, Bremerhaven. 211 pp.

FRIEDRICH, H. (1965): Meeresbiologie. – (Borntraeger) Berlin.

FROGET, C.; THOMMERET, J. & THOMMERET, Y. (1972): Mollusques septentrionaux en Méditerranée Occidentale: Datation par le ^{14}C. – Palaeogeography, Palaeoclimatology, Palaeoecology 12: 285-293.

FROUIN, R.; FIÚZA, A.; AMBAR, I. & BOYD, T.J. (1990): Observations of a poleward surface current off the coasts of Portugal and Spain in winter. – Journal of Geophysical Research (C1) 95: 679-691.

GABRIELSEN, G.W.; BREKKE, B.; ALSOS, I.G. & HANSEN, J.R. (1997). Natur og kulturmiljøet på Jan Mayen. – Norsk Polarinstitutt Meddelelser.

GAGE, J.D. (1986): The Benthic Fauna of the Rockall Trough: Regional Distribution and Bathymetric Zonation. – Proceedings of the Royal Society of Edinburgh – Series B 88: 159-174.

GAGE, J.D. (1996): Why are there so many species in deep-sea sediments? – Journal of Experimental Marine Biology and Ecology: 257-286.

GAGE, J.D. (1997): High benthic species diversity in deep-sea sediments: The importance of hydrodynamics. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V.: Marine Biodiversity. Patterns and Processes. – (Cambridge University Press) Cambridge, pp 148-177.

GAGE, J.D. & MAY, R.M. (1993): A dip into the deep seas. – Nature (London) 365: 609-610.

GAGE, J.D. & TYLER, P.A. (1991): Deep-sea biology: A natural history of organisms at the deep-sea floor. – (Cambridge University Press) Cambridge, UK.

GALLARDO, T.; GOMEZ GARETTA, A.; RIBERA, M.A.; ALVAREZ, M. & CONDE, F. (1985): A preliminary checklist of Iberian benthic marine algae. – Real Jardin Botánico, Madrid, 83 pp.

GARBARY, D.J. & G.R. SOUTH (Eds.) (1989): Evolutionary biogeography of the marine algae of the North Atlantic. – NATO ASI Series G, Vol. 22, (Springer) Berlin, 429 pp.

GARDINER, F.P. & HAEDRICH, R.L. (1978): Zonation of the deep benthic megafauna. – Oecologia 31: 311-317.

GASKIN, D.E. (1976): The evolution, zoogeography and ecology of Cetacea. – Oceanography and Marine Biology Annual Review 14: 247-346.

GEBRUK, A.G.; GALKIN, S.V.; VERESHCHAKA, A.L.; MOSKELEV, L.I. & SOUTHWARD, A.J. (1997): Ecology and Biogeography of the hydrothermal vent fauna of the Mid-Atlantic Ridge. – In: GEBRUK, A.; SOUTHWARD, E.C.& TAYLOR, P.A. (Eds.): The Biogeography of the Oceans. – Advances in Marine Biology,Vol. 32, (Academic Press) San Diego, pp 93-144.

GEBRUK, A.; SOUTHWARD, E.C. & TAYLOR, P.A. (Eds.) (1997): The Biogeography of the Oceans. – Advances in Marine Biology, Vol. 32, (Academic Press) San Diego, 596 pp.

GERMAN, C. et al. (1993): Hydrothermal activity on the Reykjanes Ridge: the Steinahóll vent field at 63°06'N. – Eos, Transactions of the American Geophysical Union 74: 360.

GERMAN, C. R. & PARSON, L.M. (1998): Distribution of hydrothermal activity along the Mid Atlantic Ridge: interplay of magmatic and tectonic controls. – Earth and Planetary Science Letters 160: 327-341.

GEORGE, R.Y. (1979): What adaptive strategies promote immigration and speciation in deep-sea environment. – Sarsia 64(1-2): 61-65.

GJØSÆTER, H. (1994): Pelagic fish and the ecological impact of the modern fishing industry in the Barents Sea. – Arctic 48: 267-278.

GJØSÆTER, H. (1997): The Barents Sea Capelin Stock (*Mallotus villosus*): a brief review. – In: Proceedings of the Role of Forage Fishes in Marine Ecosystems. – Lowell Wakefield Fisheries Symp. University of Alaska Sea Grant College Program. Report No. 97-01, pp 469-484.

GJØSÆTER, H. & USHAKOV, N.G. (1997): Acoustic Estimates of Barents Sea Arctic Cod Stock (*Boreogadus saida*). – In: Proceedings of the Role of Forage Fishes in Marine Ecosystems. – Lowell Wakefield Fisheries Symp. University of Alaska Sea Grant College Program. Report No. 97-01, pp 485-504.

GLÉMAREC, M. (1973): The benthic communities of the European North Atlantic continental shelf. Oceanogr. – Marine Biology Annual Review 11: 263-89.

GLÉMAREC, M. (1978): Distribution bathymétrique et latitudinale des bivalves du Golfe de Gascogne. – Haliotis 9: 45-48.

GLÉMAREC, M. (1979): Les fluctuations temporelles des peuplements benthiques liées aux fluctuation climatiques. – Oceanologica Acta 2: 365-371.

GLÉMAREC, M. (1988): Les facteurs déterminant la distribution des bivalves actuels sur les plates-formes Nord-Est Atlantiques. – Géologie Méditerranéenne XV(1): 73-81.

GLÉMAREC, M. (1991): Bathymetric and latitudinal distribution of Onuphid Polychaeta in the Bay of Biscay (Northeast Atlantic). – Ophelia, Supplement 5: 547-554.

GLÉMAREC, M. (1995): Classification of soft habitats in the Gulf of Gascony and English Channel. – In: HISCOCK, K. (Ed.): Classification of benthic marine biotopes of the north-east Atlantic. – Proceedings of a BioMar-Life workshop held in Cambridge, 16-18 November 1994. – Joint Nature Conservation Commitee, Peterborough, pp 102-105.

GLÉMAREC, M. (1998/2000): Groupes biogéographiques et trophiques au sein des bivalves actuels du précontinent Nord-Est Atlantique. – Unpublished tables and maps, partly presented at the "Congrès de la Réunion des Sciences de la Terre à Brest, France - 1998".

GLÉMAREC, M. & BAYED, A. (1987): La plateforme continentale atlantique nord-marocaine: bionomie et zoogéographie. – Oceanologica Acta 10(1): 111-121.

GOLIKOV, A.N. & AVERINCEV, V.G. (1977): Distribution patterns of benthic and ice biocoenoses in the high latitudes of the polar basin and their part in the biological structure of the world ocean. – In: DUNBAR, M.J. (Ed.): Polar Oceans. – Arctic Institute of North America, Calgary, pp 331-364.

GOLIKOV, A.N. & SCARLATO, O.A. (1973): Comparative characteristics of some ecosystems of the upper regions of the shelf in tropical, temperate and arctic waters. – Helgoländer Wissenschaftliche Meeresuntersuchungen 24: 219-234, Hamburg.

GOLIKOV, A.N.; DOLGOLENKO, M.A.; MAXIMOVICH, N.V. & SCARLATO, O.A. (1990): Theoretical approaches to marine biogeography. – Marine Ecology Progress Series 63: 289-301.

GORDON, J.D.M.; MERRETT, N.R. & HAEDRICH, R. L. (1995): Environmental and biological aspects of slope-dwelling fishes of the North Atlantic. – In: HOPPER, A.G. (Ed.) (1995): Deep-Water Fisheries of the North Atlantic Oceanic Slope. – Nato Advanced Science Institutes Series E – Vol. 296 (Kluwer Academic Publishers) Dordrecht, pp 1-26.

GÖTTING, K.-J.; KILIAN, E.F. & SCHNETTER, R. (1982): Einführung in die Meeresbiologie 1. Marine Organismen – Marine Biogeographie. (Vieweg) Braunschweig, 179 pp.

GOULD, W.J. (1985): Physical oceanography of the Azores Front. – Progress in Oceanography 14: 167-190.

GRAF, G. (1992). Benthic-Pelagic coupling: A benthic view. Oceanography and Marine Biology 30: 149-190.

GRAF, G.; BENGTSSON, W.; DIESNER, U.; SCHULZ, R. & THEEDE, H. (1982). Benthic response to sedimentation of a spring phytoplankton bloom processes and budget. – Marine Biology 67: 201-208.

GRAF, G.; GERLACH, S.A.; LINKE, P.; QUEISSER, W.; SCHELTZ, A.; THOMSEN, L. & WITTE, U. (1995). Benthic-Pelagic coupling in the Greenland-Norwegian Sea and its effects on the geological record. – Geologische Rundschau 84: 49-58.

GRASSHOFF, M. (1985): Die Gorgonaria, Pennatularia und Antipatharia. – In: LAUBIER, L. & MONNIOT, C. (Eds.): Peuplements profonds du Golfe de Gascogne: Campagnes BIOGAS. – (IFREMER, Service Documentation-Publications) Brest, France, pp 299-310.

GRASSLE, J.F. (1985): Hydrothermal vent animals: distribution and biology. – Science Vol. 229: 713-717.

GRASSLE, J.F. (1986): The ecology of deep-sea hydrothermal vent communities. – Advances in Marine Biology 23: 301-362.

GRASSLE, J.F. (1989): Species diversity in deep-sea communities. – Trends in Ecology and Evolution 4(1): 12-15.

GRASSLE, J.F. (1991): Deep-sea benthic biodiversity. – BioScience 41: 464-469.

GRASSLE, J.F. & MACIOLEK, N.J. (1992): Deep-sea species richness: Regional and local diversity estimates from quantitative bottom samples. – American Naturalist 139: 313-341.

GRASSLE, J.F. & SANDERS, H.L. (1973): Life histories and the role of disturbance. – Deep-Sea Research 20: 643-659.

GRASSLE, J.F.; SANDERS, H.L.; HESSLER, R.R.; ROWE, G.T. & MCLELLAN, T. (1975): Pattern and zonation: a study of the bathyal megafauna using the research submersible ALVIN. – Deep-Sea Research 22: 457-481.

GRASSLE, J.F.; SANDERS, H.L. & SMITH, W. (1979): Faunal changes with depth in the deep-sea benthos. Deep-sea ecology and exploitation. – Ambio Special Report No. 6: 47-50.

GRAY, J. & BOUCOT, A.J. (Eds.) (1979): Historical Biogeography, Plate Tectonics and the Changing Environment. – (Oregon State University Press) Corvallis, Oregon.

GREBMEIER, J.M. & BARRY, J.P. (1991): The influence of oceanographic process on pelagic-benthic coupling in polar regions: A benthic perspective. – Journal of Marine Systems 2: 495-518.

GROOMBRIDGE, B. & JENKINS, M.D. (Eds.) (1996): The diversity of the seas: A regional approach. WCMC Biodiversity Series No. 4. – World Conservation Monitoring Centre, (World Conservation Press) Cambridge, UK, 132 pp.

GUBBAY, S. (1988): A Coastal Directory for Marine Nature Conservation. – Marine Conservation Society, Ross-On-Wye, UK.

GUBBAY, S. (1995a): Marine region 5, Northeast Atlantic. – In: KELLEHER, G.; BLEAKLEY, C. & WELLS, S. (principal Eds.): A Global Representative System Of Marine Protected Areas, Vol. 1: Antarctic, Arctic, Mediterranean, Northwest Atlantic, Northeast Atlantic and Baltic. – Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN), pp 127-152.

GUBBAY, S. (Ed.) (1995b): Marine Protected Areas – Principles and Techniques for Management. Chapman and Hall, London.

GUBBAY, S. (1999): Offshore Directory. Review of a selection of habitats, communities and species of the North-East Atlantic. – Report for the WWF-UK North-East Atlantic Programme, 77 pp.

GUDMANDSEN, P.; PEDERSEN, L.T.; SKRIVER, H.; THOMSEN, B.B. & MINNETT, P.J. (1993): Radar observations of an Arctic polynya under summer conditions. – Proceedings of the Second ERS-1 Symposium – Space at the Service of our Environment, Hamburg, Germany, 11-14 October 1993. ESA SP-361.

GUDMANDSEN, P. & THOMSEN, B.B. (1994): Satellite Data from the North-East Water polynya, June-August 1993. – Elektromagnetics Institute, Lyngby Denmark, Report R 568, 118 pp.

GUDMANDSEN, P.; THOMSEN, B.B. & MINNETT, P.J. (1995): North-East Water polynya: Satellite observations summer 1992 & 1993. – International Journal of Remote Sensing 16: 3307-3324

GUENNEGAN, Y. & RANNOU, M. (1979): Semi-diurnal rhythmic activity in deep-sea benthic fishes in the Bay of Biscay. – Sarsia 64: 113-116.

GULLIKSEN, B. (1984): Under-ice fauna from Svalbard waters. Sarsia 69: 17-23.

GULLIKSEN, B. & LØNNE, O.J. (1989): Distribution, abundance and ecological importance of marine sympagic fauna in the Arctic. – Rapports et Procès-Verbaux des Réunions. Conseil Internationale pour l'Exploration de la Mer 188: 133-138.

GULLIKSEN, B.; PALLERUD, R.; BRATTEGARD, T. & SNELI, J. (EDS.) (1999): Distribution of marine benthic macro-organisms at Svalbard (including Bear Island) and Jan Mayen. – Research Report for DN Nr. 1999-4. Direktoratet for Naturforvaltning, Trondheim, 148 pp.

HAACK (Ed.) (1989): Atlas Weltmeer. – (VEB Hermann Haack Geographisch-Kartographische Anstalt Gotha), Gotha, DDR.

HÅKANSSON, E.; BENNIKE, O.; MØLGAARD, P. & FRYKMAN, P. (1981): Bird observations from northern Greenland in the summers of 1976 and 1978. – Dansk Ornitologisk Forenings Tidsskrift 75: 51-67.

HAEDRICH, R.L. & JUDKINS, D.C. (1979): Macrozooplankton and its environment. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 4-28.

HAEDRICH, R.L. & KREFFT, G. (1978): Distribution of bottom fishes in the Denmark Straits and Irminger Sea. – Deep-Sea Research 25: 707-720.

HAEDRICH, R.L. & MERRETT, N.R. (1988): Summary atlas of deep-living fishes in the North Atlantic Basin. – Journal of Natural History 22: 1325-1362.

HAEDRICH, R.L. & MERRETT, N.R. (1990): Little evidence for faunal zonation or communities in the deep demersal fish fauna. – Progress in Oceanography 24: 239-250.

HALL, C. (1964): Shallow-water marine climates and molluscan provinces. – Ecology 45(2): 226-234.

HALLAM, A. (Ed.) (1973): Atlas of palaeobiogeography. – (Elsevier Scientific Publishers) Amsterdam, 531 pp.

HALLAM, A. (1981): Relative importance of plate movements, eustasy, and climate in controlling major biogeographical changes since the early Mesozoic. – In: NELSON, G. & ROSEN, D.E. (Eds.): Vicariance Biogeography: A Critique. – (Columbia University Press) New York, pp 303-330.

HANSEN, B. (1967): The taxonomy and zoogeography of the deep-sea holothurians in their evolutionary aspects. – Studies in Tropical Oceanography, Miami 5: 480-501.

HANSEN, B. (1985): The circulation of the northern part of the North east Atlantic. – Rit Fiskideildar 9: 110-126.

HANSEN, J.R.; HANSSON, R. & NORRIS, S. (1996): The state of the European Arctic Environment. – EEA Environmental Monograph No. 3, 136 pp. – also published as: Norsk Polarinstittut Meddelelser No. 141.

HAQ, B.U.; PREMOLI-SILVA, I. & LOHMANN, G.P. (1977): Calcareous plankton paleobiogeographic evidence for major climatic fluctuations in the Early Cenozoic Atlantic Ocean. – Journal of Geophysical Research 82: 3861-3876.

HAQ, B.U. (1984): Paleoceanography: a synoptic overview of 2000 million years of ocean history. – In: HAQ, B.U. & MILLIMAN, H.D. (Eds.): Marine Geology and Oceanography of Arabian Sea and Coastal Pakistan. – (Van Nostrand Reinhold) New York, pp 201-231.

HARDY, A.C. (1956): The Open Sea, It's Natural History. Part I: The World of Plankton. – (Collins) London.

HARDY, A.C. (1958): The Open Sea. – (Houghton Mifflin) Boston, 335 pp.

HARDY, A.C. (1971 a): The open sea: Part I. The World of Plankton. Revis. Ed., – (Collins) London.
HARDY, A.C. (1971 b): The open sea: it's natural history. Part II. Fish and fisheries. New Ed., – (Collins) London.
HARGREAVES, P.M. (1984): The distribution of Decapoda (Crustacea) in the open ocean and near-bottom over an adjacent slope in the northern North-East Atlantic Ocean during autumn 1979. – Journal of the Marine Biological Association of the United Kingdom 64(4): 829-857.
HARGREAVES, P.M. (1985): The distribution of Mysidaceae in the open ocean and near-bottom over slope regions in the northern North-East Atlantic Ocean during 1979. – Journal of Plankton Research 7(2): 241-261.
HARGREAVES, P.M.; ELLIS, C.J. & ANGEL, M.V. (1984): An assessment of biological processes close to the sea-bed in a slope region and its significance to the assessment of sea-bed disposal of radioactive waste. – Institute of Oceanographic Science Report, No. 185, 121 pp.
HASSEL, A. (1986): Seasonal changes in zooplankton composition in the Barents Sea, with special attention to Calanus spp. (Copepoda). – Journal of Plankton Research 8: 329-339.
HAURY, L.R.; MCGOWAN, J.A. & WIEBE, P.H. (1978): Patterns and Processes in the Time-Space Scales of Plankton Distributions. – In: STEELE, J.H. (Ed.): Spatial Patterns in Plankton Communities. – (Plenum Press) New York, pp 277-327.
HAYDEN, B.P.; RAY, G.C. & DOLAN, R. (1984): Classification of Coastal and Marine Environments. – The Foundation for Environmental Conservation, Switzerland – Environmental Conservation Vol. 11, No. 3, Autumn 1984.
HECKER, B. (1990): Variation in megafaunal assemblages on the continental margin south of New England. – Deep-Sea Research 37A: 37-57.
HEDGEPETH, J.W. (1957a): Classification of marine environments. – In: HEDGEPETH, J.W. (Ed.): Treatise on marine ecology and paleoecology. – Geological Society of America, Memoir 67, Vol. 1, pp 17-27.
HEDGEPETH, J.W. (1957 b): Marine biogeography. – In: HEDGEPETH, J.W. (Ed.): Treatise on marine ecology and paleoecology. – Geological Society of America, Memoir 67, Vol. 1, pp 359-382.
HELA, I. & T. LAEVASTU (1961): Fisheries hydrography. – (Fishing News (Books) LTD) London.
HELCOM (1994): Recommendation 15/5. System of coastal and marine Baltic Sea Protected Areas (BSPA). – In: BUNDESANZEIGER, Jahrgang 48 Nr. 50a, 4.1.1996: Bekanntmachung der Empfehlungen HELCOM 15/1–15/5 der Kommission zum Schutz der Meeresumwelt des Ostseegebiets – Helsinki-Kommission, pp 8-10. – or: http://www.helcom.fi/fullrecs/rec15_5.html
HELLUM, C. (1994): Phytoplankton and ice algae. Species composition. – In: HIRCHE, H.-J. & KATTNER, G. (Eds.): The 1993 Northeast Water Expedition scientific cruise report of RV "Polarstern" Arctic cruises ARK IX/2 and 3, USCG "Polar Sea" cruise NEWP and the NEWLand expedition. – Berichte zur Polarforschung 142, pp 67-72.
HEMPEL, G. (1985): On the biology of polar seas, particularly the Southern Ocean. – In: GRAY, J.S. & CHRISTIANSEN, M.E. (Eds.): Marine biology of polar regions and effects of stress on marine organisms. – Proceedings of the 18th European Marine Biology Symposium, Oslo, Norway, 14-20 August 1983. – (John Wiley & Sons) Chichester, pp 3-33.
HENRICH, R.; WAGNER, T.; GOLDSCHMIDT, P. & MICHELS, K. (1995): Depositional regimes in the Norwegian-Greenland Sea: the last two glacial to interglacial transitions. – Geologische Rundschau 84: 28-48.
HERMAN, Y. (1974): Topography of the Arctic Ocean. – In: HERMAN, Y. (Ed.): Marine Geology and Oceanography of the Arctic Seas. – (Springer) Berlin, pp 73-82.
HERMAN, Y. (1979): Plankton distribution in the past. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 29-49.
HERMAN, Y. & HOPKINS, D.M. (1980): Arctic oceanic climate in the Late Cenozoic time. Science 209: 457-462.
HESSE, R.; ALLEE, W.C. & SCHMIDT, K.P. (1937/1951): Ecological Animal Geography. (1st/2nd edn.). – (John Wiley & Sohns) New York, NY, USA.
HESSLER, R.R. & H.L. SANDERS (1967): Faunal diversity in the deep-sea. – Deep-Sea Research 14: 65-78.

HESSLER, R.R. & THISTLE, D. (1975): On the place of origin of deep-sea isopods. – Marine Biology 32: 155-165.

HESSLER, R.R.; WILSON, G.D.F. & THISTLE, D. (1979): The deep-sea isopods: A biogeographic and phylogenetic overview. – Sarsia 64: 67-75.

HESSLER, R.R. & WILSON, G.D.F. (1983): The Origin and Biogeography of Malacostracan Crustaceans in the Deep Sea. – In: SIMS, R.W.; PRICE, J.H & WHALLEY, P.E.S. (Eds.): Evolution, Time and Space: The Emergence of the Biosphere. – The Systematics Association Special Volume No. 23. – (Academic Press) London, pp 227-254.

HIRCHE, H.-J.; BAUMANN, M.; KATTNER, G. & GRADINGER, R. (1991): Plankton distribution and the impact of copepod grazing on primary production in Fram Strait. – Journal of Marine Systems 2: 477.

HIRCHE, H.-J. & DEMING, J.W. (Eds.) (1997): Northeast Water Polynya Symposium. – Journal of Marine Systems 10 (1-4). 520 pp.

HIRCHE, H.-J. & KATTNER, G. (Eds.) (1994): The 1993 Northeast Water Expedition scientific cruise report of RV "Polarstern" Arctic cruises ARK IX/2 and 3, USCG "Polar Sea" cruise NEWP and the NEWLand expedition. – Berichte zur Polarforschung 142: 1-190.

HISCOCK, K. (1985): Aspects of the ecology of rocky sublittoral areas. – In: MOORE, P.G. & SEED, R. (Eds.): The ecology of rocky coasts: essays presented to J.R. Lewis D.Sc. – (Hodder and Stoughton) London, pp 290-328.

HISCOCK, K. (1991): Benthic marine ecosystems in Great Britain: A review of current knowledge. Introduction and Atlantic-European Perspective. – Nature Conservancy Council, CSD Report No.1170. Nature Conservancy Council, Peterborough. (MNCR Report, No. MNCR/OR/6).

HISCOCK, K. (Ed.) (1995): Classification of benthic marine biotopes of the north-east Atlantic. Proceedings of a BioMar-Life workshop held in Cambridge, 16-18 November 1994. – Joint Nature Conservation Commitee, Peterborough.

HISCOCK, K. (Ed.) (1996): Rationale and methods. Coast and Seas of the United Kingdom. – Marine Nature Conservation Review series. – Joint Nature Conservation Committee (JNCC), Peterborough, U.K., 167 pp.

HISCOCK, K. (1997): Conserving biodiversity in North-East Atlantic marine ecosystems. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V.: Marine Biodiversity. Patterns and Processes. – (Cambridge University Press) Cambridge, pp 415-427.

HISCOCK, K. (Ed.) (1998): Benthic marine ecosystems of Great Britain and the north-east Atlantic. – Marine Nature Conservation Review series. – Joint Nature Conservation Committee (JNCC), Peterborough, U.K., 404 pp.

HJORT, C.; HÅKANSSON, E. & STEMMERIK, L. (1983): Bird observations around the Nordøstvandet polynya, Northeast Greenland, 1980. – Dansk Ornitologisk Forenings Tidsskrift 77: 107-114.

HJORT, C.; HÅKANSSON, E. & MØLGAARD, P. (1987): Brent Geese Branta bernica, Snow Geese Anser caerulescens and Barnacle Geese Branta leucopsis on Kilen, Kronprins Christian Land, Northeast Greenland, 1985. – Dansk Ornitologisk Forenings Tidsskrift 81: 121-128.

HJORT, C.; HÅKANSSON, E. & MØLGAARD, P. (1988): Bird observations on Kilen, northeasternmost Greenland, 1985. – Dansk Ornitologisk Forenings Tidsskrift 82: 19-24.

HØISAETER, T. (1986): A annotated check-list of marine molluscs of the Norwegian coast and adjacent waters. – Sarsia 71: 73-145.

HOLLIGAN, P.M. (1978): Patchiness in subsurface phytoplankton populations on the northwest European continental shelf. – In: STEELE, J.H. (Ed.): Spatial Patterns in Plankton Communities. – (Plenum Press) New York, pp 221.

HOLLIGAN, P.M. (1981): Biological implication of fronts of the northwest European continental shelf. – Philosophical Transactions of the Royal Society of London. Series A, Vol. 302: 547-562.

HOLME, N.A. (1961): The bottom fauna of the English Channel. – Journal of the Marine Biological Association of the United Kingdom 41: 397-461.

HOLME, N.A. (1966): The bottom fauna of the English Channel II. – Journal of the Marine Biological Association of the United Kingdom 46: 401-493.

HOLME, N.A. & REES, E.I.S. (1986): An interesting deep water community in the Irish Sea. – Challenger Society Newsletter 22: 15.

HOLTHE, T. (1978): The zoogeography of the Terebellomorpha (Polychaeta) of the northern European waters. – Sarsia 63: 191-198.
HÖLZEL, Ed. (Ed.) (1998): Resources and Environment World Atlas, Part II. – (Institute of Geography–Russian Academy of Science/IG RAS) Moscow & (Ed. HÖLZEL) Vienna.
HOMMERSAND, M.H (1989): Biogeography of the Marine Red Algae of the North Atlantic Ocean. – In: GARBARY, D.J. & SOUTH, G.R.: Evolutionary biogeography of the marine algae of the North Atlantic. – (Springer) Berlin, pp 349-410.
HORNER, R.A. (1985a): History of ice algal investigations. – In: HORNER, R.A. (Ed.): Sea Ice Biota. – (CRC Press) Boca Raton, Florida, pp 2-19.
HORNER, R.A. (1985b): Ecology of Sea Ice Microalgae. – In: HORNER, R.A. (Ed.): Sea Ice Biota. – (CRC Press) Boca Raton, Florida, pp 83-103.
HORNER, R.A. (1990): Ice-associated ecosystems. – In: MEDLIN, L.K. & PRIDDLE, J. (Eds.): Polar marine diatoms. – British Antarctic Survey, Cambridge, pp 9-14.
HORNER, R.; ACKLEY, S.F.; DIECKMANN, G.S.; GULLIKSEN, B.; HOSHIAI, T.; LEGENDRE, L.; MELNIKOV, I.A.; REEBURGH, W.S.; SPINDLER, M. & SULLIVAN, C.W. (1992): Ecology of sea ice biota. 1.) Habitat, terminology, and methodology. – Polar Biology 12: 417-427.
HOVGÅRD, H. & BUCH, E. (1992): Fluctuation in the Cod Biomass of the West Greenland Sea Ecosystem in Relation to Climate. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large marine ecosystems: patterns, processes and yields. – American Association for the Advancement of Science, Washington DC, USA, pp 36-43.
HOVLAND, M.; MORTENSEN, P.B.; BRATTEGARD, T.; STRASS, P. & ROKOENGEN, K. (1998): Ahermatypic coral banks off mid-Norway: evidence for a link with seepage of light hydrocarbons. – Palaios 13: 189-200.
HULT, J. (1941): On the soft-bottom isopods of the Skagerrak. – Zoologiska bidrag van Uppsala 21: 1-234.
HUNT, G.L. jr. (1991): Marine birds and ice-influenced environments of polar oceans. – Journal of Marine Systems 2: 233-240.
HURDLE, B.G. (Ed.) (1986): The Nordic Seas. – (Springer) Berlin.
HUREAU, J.C. & MONOD, TH. (Eds.) (1973): Check-list of the fishes of the north-eastern Atlantic and of the Mediteranean (CLOFNAM). Vol. 1:1-683. – UNESCO, Paris.
HUTCHINS, L.W. (1947): The bases for temperature zonation in geographical distribution. – Ecological Monographs 17: 325-335.
IBÁÑEZ, M.; MIGUEL, I.; SAN MILLÁN, M.D. & RIPA, M.I. (1989): Intertidal ichtyofauna of the Spanish Atlantic coast. – In: ROS, J.D. (Ed.): Topics in Marine Biology. 22nd European Marine Biology Symposium. – Scientia Marina 53: 451-455.
INGÓLFSON, A. (1996): The distribution of intertidal Macrofauna of the coasts of Iceland in relation to temperature. – Sarsia 81: 29-44.
IRVINE, D.E.G. (1974): The marine vegetation of the Shetland Isles. – In: The natural environment of Shetland. – NCC, Edinburgh, pp 107-113.
IRVINE, D.E.G. (1982): Seaweeds of the Faroes. I: The flora. Bull. Br. Mus. nat. Hist. (Bot.) 10: 109-131.
IRVINE, D.E.G.; SMITH, R.M.; TITTLEY, I.; FLETCHER, R.L. & FARNHAM, W.F. (1982): Seaweeds of the Faroes. – British Phycological Journal 17: 234.
JABLONSKI, D. & VALENTINE, J.W. (1990): From regional to total geographical ranges: testing the relationship in recent Bivalvia. – Paleobiology 16: 126-142.
JABLONSKI, D.; D.H. ERWIN & J.H. LIPPS (Eds.) (1996): Evolutionary Paleobiology. In honor James W. Valentine. – (University of Chicago Press) Chicago and London, 484 pp.
JANNASCH, H.W. & MOTTL, M.J. (1985): Geomicrobiology of Deep-Sea Hydrothermal Vents. – Science Vol. 229: 717-725.
JENSEN, A. & FREDERIKSEN, R. (1992): The fauna associated with the bank forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. – Sarsia 77: 53-69.
JOHNSON, C.G. & SMITH, L.P. (Eds.) (1965): The biological significance of climate changes in Britain. – Institute of Biology Symposia, No. 14, (Academic Press) London.
JONES, A.M. (1975): The marine environment of Orkney. – In: GOODIER, R. (Ed.): The natural environment of Orkney. – NCC, Edinburgh, pp 85-94.

JONES, E.J.W.; SIDDALL, R.; THIRLWALL, M.F.; CHROSTON, P.N. & LLOYD, A.J. (1994): Anton Dohrn Seamount and the evolution of the Rockall Trough. – Oceanologica Acta 17(3): 237-247.

JONES, L.T. (1963): The geographical and vertical distribution of British Limnoria (Crustacea: Isopoda). – Journal of the Marine Biological Association of the United Kingdom 43: 589-603.

JUMARS, P.A. (1976): Deep-Sea diversity–does it have a characteristic scale? – Journal of Marine Research 34: 217-246.

JUMARS, P.A. & ECKMAN, J.E. (1983): Spatial structure within deep-sea benthic communities. – In: ROWE, G.T. (Ed.): Deep-Sea Biology. The Sea, Vol. 8. – (John Wiley & Sons) New York, pp 399-451.

JUST, J. (1980a): Abyssal and deep bathyal Malacostraca (Crustacea) from the Polar Sea. – Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 142: 161-177.

JUST, J. (1980b): Polar Sea abyssal and deep bathyal Isopoda (Crustacea). – Steenstrupia 6: 197-230.

KATONA, S.K. (1986): Biogeography of the Humpback Whale, *Megaptera novaeangliae*, in the North Atlantic. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. UNESCO technical papers in marine science no. 49, Paris, pp 166-171.

KAUFFMAN, E.C. (1973): Cretacous bivalvia. – In: HALLAM, A. (Ed.): Atlas of palaeobiogeography. – (Elsevier Scientific Publishers) Amsterdam, pp 353-335.

KELLEHER, G.; BLEAKLEY, C. & WELLS, S. (principal Eds.) (1995): A Global Representative System Of Marine Protected Areas, Vol. 1: Antarctic, Arctic, Mediterranean, Northwest Atlantic, Northeast Atlantic and Baltic. – Great Barrier Reef Marine Park Authority, The World Bank, The World Conservation Union (IUCN).

KELLEHER, G. (Ed.) (1999): Guidelines for Marine Protected Areas. – World Commission on Protected Areas of IUCN–The World Conservation Union. Best Practice Protected Area Guidelines Series No. 3. Gland, Switzerland and Cambridge, UK., 107 pp.

KELLETAT, D.H. (1995): Atlas of coastal geomorphology and zonality. – Journal of Coastal Research; special issue 13. Fort Lauderdale, CERF, 286 pp.

KENDALL, M.A. & ASCHAN, M. (1993): Latitudinal gradients in the structure of macrobenthic communities: a comparison of Arctic, temperate and tropical sites. – Journal of Experimental Marine Biology and Ecology 172:157-169.

KENNETT, J. (1982): Marine Geology. – (Prentice Hall) Englewood Cliffs, New Jersey. 873 pp.

KENYON, N.H.; IVANOV, M.K. & AKHMETZHANOV, A.M. (1998): Cold Water Carbonates Mounds and Sediment Transport on the NE Atlantic Margin. – Intergovernmental Oceanographic Commission, IOC Technical Report 52.

KINNE, O. (Ed.) (1970): Marine Ecology, Vol. I: Environmental factors. Part 1. – (Wiley-Interscience) London.

KINNE, O. (Ed.) (1982, 1983, 1984): Marine Ecology, Vol. V - Ocean Management, Part 1- 4. – (John Wiley & Sons) Chichester, New York, Brisbane, Toronto, Singapore.

KIRKEGAARD, J.B. (1954): The zoogeography of the abyssal Polychaeta. – In: INTERNATIONAL UNION OF BIOLOGICAL SCIENCES: On the distribution and Origin of the Deep Sea Bottom Fauna., Series B 16, Naples, pp 40-43.

KLEINE, B & SIEDLER, G. (1989): On the origin of the Azores current. – Journal of Geophysical Research (C. Oceans) 94(C5): 6159-6168.

KNUDSEN, J. (1970): The systematics and biology of abyssal and hadal bivalvia. – Galathea Report 11: 7-236.

KNUDSEN, J. (1985): Abyssal Mollusca of the Arctic Ocean. – Journal of Conchology 32: 97-107.

KOSLOW, J.A. & GOWLETT-HOLMES, K. (1998): The seamount fauna of southern Australia: benthic communities, their conservation and impacts of trawling. – Report to Environment Australia and the Fisheries Research Development Corporation. FRDC Project 95/058.

KOSLOW, J.A.; BOEHLERT, G.W.; GORDON, J.D.M.; HAEDRICH, R.L.; LORANCE, P. & PARIN, N. (1999): The Impact of Fishing on Continental Slope and Deep-sea ecosystems. The impact of fishing on continental slope and deep-sea ecosystems. A review presented at the SCOR Symposium on the Ecosystem Impacts of Fishing. Montpellier, France, 16-19 March 1999. – ICES Journal of Marine Sciences.

KOTTHAUS, A. & KREFFT, G. (1967): Observations on the distribution of demersal fish on the Iceland-Faroe Ridge in relation to bottom temperatures and depths. – Rapports et Procès-Verbaux des Réunions. Conseil Internationale pour l'Exploration de la Mer 157: 238-276.

KOUTSIKOPOULOS, C. & LE CANN, B. (1996): Physical processes and hydrological structures related to the Bay of Biscay anchovy. – Scientia Marina 60 (Suppl. 2): 9-19.

KRAUSE, D.C. & ANGEL, M.V. (1994): Marine biogeography, climate change and societal needs. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 221-235.

KREYSCHER, M.(1998): Dynamik des arktischen Meereises–Validierung verschiedener Rheologieansätze für die Anwendung in Klimamodellen. – Berichte zur Polarforschung Vol. 291, Bremerhaven. 116 pp.

KRÖNKE, I. (1992): Macrofauna standing stock of the Dogger Bank. A comparison: III. 1950-54 versus 1985-87. A final summary. – Helgoländer Meeresuntersuchungen 46: 137-169.

KÜNITZER, A.; BASFORD, D.; CRAEYMEERSCH, J.A.; DEWARUMEZ, J.M.; DÖRJES, J.; DUINEVELD, G.C.A.; ELEFTHERIOU, A.; HEIP, C.; HERMAN, P.; KINGSTON, P.; NIERMANN, U.; RACHOR, E.; RUMOHR, H. & DE WILDE, P.A.J. (1992): The benthic fauna of the North Sea: species distribution and assemblages. – ICES Journal of Marine Sciences 49: 127-143.

KUSSAKIN, O.G. (1973): Peculiarities of the geographical and vertical distribution of marine isopods and the problem of deep-sea fauna origin. – Marine Biology 23: 19-34.

KVAMBEKK, Å.S. & VINJE, T. (1993): The ice transport through Fram Strait. – Nansen Centennial Symposium, Bergen, Norway, 21-25 June 1993.

LAEVASTU, T. (1961): Natural bases of fisheries in the Atlantik Ocean: Their past and present characteristics and possibilities for future expansion. – In: BORGSTROM, G. & HEIGHWAY, A.J. (Eds.): Atlantik Ocean Fisheries. – (Fishing News Books Ltd.) Surrey, UK, pp 18-39.

LAFFOLEY, D. d'A; BAXTER, J.; BINES, T.; BRADLEY, M.; CONNOR, D.W.; HILL, M.; TASKER, M.; & VINCENT, M. (2000a): Nationally important seascapes, habitats and species. Prepared for the DETR Working Group on the Review of Marine Nature Conservation by English Nature and the Joint Nature Conservation Commitee. Peterborough, English Nature Science Report 392, 17 pp.

LAFFOLEY, D. d'A; M.; CONNOR, D.W.; TASKER, M.; & BINES, T. (2000b): An implementation for conservation, protection and management of nationally important marine wildlife in the UK. Prepared by the statutory nature conservation agencies, Environment Heritage Services (Northern Ireland) and JNCC for the DETR Working Group on the Review of Marine Nature Conservation. Peterborough, English Nature Science Report 394, 29 pp.

LAMBSHEAD, P.J.D.; FERRERO, T.J. & WOLFF, G.A. (1995): Comparison of the vertical Distribution of Nematodes from Two Contrasting Abyssal Sites in the Northeast Atlantic: Subject to Different Seasonal Inputs of Phytodetritus. – Internationale Revue der gesamten Hydrobiologie, Volume 80, No. 2: 327-331.

LAMI, R. (1931): Sur la répartition géographique de quelques Algues marines dans la région Nord des côtes du Portugal. – C. R. A. S., t. 193: p. 1442.

LAMI, R. (1933): Sur la végétation des Algues marines dans la région Sud des côtes du Portugal. – C. R. A. S., t. 197: pp. 83-85.

LAMPITT, R.S. & ANTIA, A.N. (1997): Particle flux in the deep seas: regional characteristics and temporal variability. – Deep-Sea Research I 44(8): 1377-1403.

LARA, R.T. ; KATTNER, G.; TILLMANN, U. & HIRCHE, H.-J. (1994): The North East Water Polynya (Greenland Sea) II. Mechanisms of nutrient supply and influence on phytoplankton distribution. – Polar Biology 14: 483-490.

LAUBIER, L. & MONNIOT, C. (Eds.) (1985): Peuplements profonds du Golfe de Gascogne: Campagnes BIOGAS. – (IFREMER, Service Documentation-Publications) Brest, France, 629 pp.

LAUBIER, L. & SIBUET, M. (1977): Ecology of the benthic communities of the deep North East Atlantic. – Ambio, Special Report 6 : 37-42.

LAWSON, G.W. (1978): The distribution of seaweed floras in the tropical and subtropical Atlantic Ocean: A quantitative approach. – Botanical Journal of the Linnean Society 76: 177-193.

LEAN, G. (1982): A Network to Save the Seas: UNEP's Regional Seas Programme. – IUCN Bulletin 13 (4-5-6): 39.

LEE, A.J. (1970): The currents and water masses of the North Sea. – Oceanography and Marine Biology Annual Review 8: 33-71.

LEE, A.J. & RAMSTER, J.W. (1981): Atlas of the Seas around the British Isles. – Compiled by the Directorate of Fisheries Research, Ministry of Agriculture, Fisheries and Food. Lowestoft, Suffolk.

LE DANOIS, Ed. (1948): Les Profondeurs de la Mer. Trente ans de recherches sur la fauna sousmarine au large des côtes de France. – (Payot) Paris, 303 pp.

LEGECKIS, R. (1978): A survey of worldwide sea surface temperature fronts detected by environmental satellite. – Journal of Geophysical Research 83: 4501-4522.

LEGENDRE, L.; ACKLEY, S.F.; DIECKMANN, G.S.; GULLIKSEN, B.; HORNER, R.; HOSHIAI, T.; MELNIKOV, I.A.; REEBURGH, W.S.; SPINDLER, M.& SULLIVAN, C.W. (1992): Ecology of sea Ice Biota. 2.) Global significance. – Polar Biology 12: 429-444.

LEVIN, L. & GAGE, J.D. (1998): Relationship between oxygen, organic matter and the diversity of bathyal macrofauna. – Deep-Sea Research II 45: 129-163.

LLORIS, D.; J. RUCABADO & H. FIGUEROA (1991): Biogeography of the Macaronesian ichtyofauna (The Azores, Madeira, the Canary Islands, Cape Verde and the African enclave). – Boletim do Museu Municipal do Funchal 43(234): 191-241.

LOENG, H. (1991): Features of the physical oceanographic conditions of the Barents Sea. – Polar Research 10: 5-18.

LØNNE, O.J. & GULLIKSEN, B. (1991a): On the distribution of sympagic macro-fauna in the seasonally ice covered Barents Sea. – Polar Biology 11: 457-469.

LØNNE, O.J. & GULLIKSEN, B. (1991b): Sympagic macro-fauna from multiyear sea ice near Svalbard. – Polar Biology 11: 471-477.

LONGHURST, A. (1995): Seasonal cycles of pelagic production and consumption. – Progress in Oceanography 36: 77-167.

LONGHURST, A. (1998): Ecological Geography of the Sea. – (Academic Press) San Diego, 398 pp.

LOVÉN, S. (1846): Malakologiska notiser. Nagra anmärkningar öfver de Skandinaviska Hafs Molluskernas geografiska utbredning. – Övers K. Svenska. Vet.-Acad. Förhandl. Stockholm, pp 252-274.

LOZÁN, J.L. (Ed.) (1990): Warnsignale aus der Nordsee. – (Parey) Berlin, 431 pp.

LOZÁN, J.L.; RACHOR, E.; REISE, K.; VON WESTERNHAGEN, H. & LENZ, W. (Eds.) (1994): Warnsignale aus dem Wattenmeer. – (Blackwell) Berlin.

LUCAS, C.E. & GLOVER, R.S. (Eds.) (1973): Continuous Plankton Records: A Plankton Atlas of the North Atlantic and the North Sea, by the Oceanographic Laboratory, Edinburgh. – Bulletins of Marine Ecology, Vol. VII. The Institute for Marine Environmental Research, Plymouth, 174 pp.

LÜNING, K. (1985): Meeresbotanik. – (Georg Thieme Verlag) Stuttgart, New York, 375 pp.

LÜNING, K. (1990): Seaweeds: Their Environment, Biogeography and Ecophysiology. – (John Wiley & Sons) New York.

MACIOLEK, N.J.; GRASSLE, J.F.; HECKER, B.; BOEHM, P.D.; BROWN, B.; DADE, B.; STEINHAUER, G.; BAPTISTE, E.; RUFF, R.E. & PETRECCA, R. (1987a): Study of biological processes on the U.S. mid-Atlantic slope and rise. – Final report prepared for U.S. Department of the Interior, Minerals Management Service, Washington, D.C.

MACIOLEK, N.J.; GRASSLE, J.F.; HECKER, B.; BROWN, B.; BLAKE, J.A.; BOEHM, P.D.; PETRECCA, R.; DUFFY, S.; BAPTISTE, E. & RUFF, R.E. (1987b): Study of biological processes on the U.S. North Atlantic slope and rise. – Final report prepared for U.S. Department of the Interior, Minerals Management Service, Washington, D.C.

MACKIE, A.S.Y. (1990): Offshore benthic communities of the Irish Sea. – In: IRISH SEA STUDY GROUP (Eds.): The Irish Sea: an environmental review. Part One: Nature Conservation. – Liverpool University Press for Irish Sea Study Group, Liverpool, pp 169-218.

MACKIE, A.S.Y; OLIVER, P.G. & REES, E.I.S. (1995): Benthic biodiversity in the southern Irish Sea. – Studies in Marine Biodiversity and Systematics from the National Museum of Wales. BIOMÔR Reports 1, 263 pp.

MADSEN, F.J. (1961): On the zoogeography and origin of the abyssal fauna – in view of the knowledge of the Porcellanasteridae. – In: WOLFF, T. (Ed.): Galathea Report, Vol. 4. – (Danish Science Press Ltd) Copenhagen, pp 177-218.

MADSEN, H. (1936): Investigations on the shore fauna of East Greenland with a survey of the shores of other Arctic regions. – Meddelelser om Grønland 100(8): 1-79.

MAGNÚSSON, J.V. & MAGNÚSSON, J. (1995): The distribution, relative abundance and the biology of the deep-sea fishes of the Icelandic slope and Reykjanes Ridge. – In: HOPPER, A.G. (Ed.): Deep-Water Fisheries of the North Atlantic Oceanic Slope. – Nato Advanced Science Institutes Series E–Vol 296, (Kluwer Academic Publishers) Dordrecht, pp 161-200.

MAGNÚSSON, J. (1996): The deep scattering layers in the Irminger Sea. – Journal of Fish Biology 49, Supplement A: 182-191.

MALATESTA, A. & ZARLENGA, F. (1986): Northern guests in the Pleistocene Mediterranean Sea. – Geologica Romana 25: 91-154.

MALMBERG, S.-A. (1985): The water masses between Iceland and Greenland. – Rit Fiskideildar 9: 127-140.

MALMBERG, S.-A. (1986): The ecological impact of the East Greenland Current on the north Icelandic waters. – In: SKRESLET, S. (Ed.): The role of freshwater outflow in coastal marine ecosystems. – NATO ASI series, Vol. G7. (Springer) Berlin, pp 389-404.

MALMBERG, S.-A. & KRISTMANNSSON, S.S. (1992): Hydrographic condition in Icelandic waters, 1980-1989. – ICES mar. Sci. Symp. 195: 76-92.

MANN, C.R. (1967): The termination of the Gulf Stream and the beginning of the North Atlantic Current. – Deep-Sea Research 14: 337-359.

MARINCOVICH, L. jr.; BROUWERS, E.M.; HOPKINS, D.M. & MCKENNA, M.C. (1990): Late Mesozoic and Cenozoic paleogeographic and paleoclimatic history of the Arctic Ocean Basin, based on shallow-water marine faunas and terrestrial vertebrates. – In: GRANTZ, A.; JOHNSON, L. & SWEENEY, J.F. (Eds.): The geology of North America, Vol. L., The Arctic Ocean region. – The Geological Society of America, Boulder, Colorado, pp 403-426.

MARSHALL, N.B. (1982): Glimpses into deep-sea biology. – In: REY, L. & STONEHOUSE, B. (Ed.): The Arctic Ocean. The hydrographic environment and the fate of pollutants. – (Macmillan Press Ltd.) London, UK.

MARKUS, T. & BURNS, B.A. (1995): A method to estimate subpixel-scale coastal polynyas with satellite passive microwave data. – Journal of Geophysical Research 100(3): 4473.

MASSOM, R.A. (1988): The biological significance of open water within sea ice covers of the polar regions. – Endeavour 12: 21-27.

MAUCHLINE, J. (1986): What constitutes an open-ocean population. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, pp 186-190.

MAUCHLINE, J. (1990): Aspects of production in a marginal oceanic region, the Rockall Trough, northeastern Atlantic Ocean. – Reviews in Aquatic Sciences 2: 167-183.

MAYCAS, E.R.; BOURDILLON, A.; MACQUART-MOULIN, C.; PASSELAIGUE, F. & PATRITI, G. (1999): Diel variations of the bathymetric distribution of zooplankton groups and biomass in Cap-Ferret Canyon, France. – Deep-Sea Research II 46: 2081-2099.

MAYKUT, G.A. (1985): The Ice Environment. – In: HORNER, R.A. (Ed.): Sea Ice Biota. – (CRC Press) Boca Raton, Florida, pp 21-82.

MCARTHUR, R.H. & WILSON, E.O. (1967): The Theory of Island Biogeography. – (Princeton University Press) Princeton, New Jersey, 203 pp.

MCARTHUR, R.H. (1972): Geographical Ecology: Patterns in the Distribution of Species. – (Harper & Row) New York, NY, USA. 269 pp.

MC GOWAN, J.A. (1985): The biogeography of pelagic ecosystems. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, pp 191-200.

MCCONNAUGHEY, B.H. (1974): Zoogeography of the seas. chap. 12 – In: MCCONNAUGHEY, B.H.: Introduction to Marine Biology. (2nd ed.). – (The C. V. Mosby Company) St. Louis, pp 307-336.

MCINTYRE, A. & BÉ, A.W. H. (1967): Modern Coccolithophoridea of the Atlantic Ocean. I. Placoliths and cyrtoliths. Deep-Sea Research 14: 561-597.

McINTYRE, A.; KIPP, N.G.; BÉ, A.W.H.; COWLEY, T.; KELLOG, T.; GARDNER, J.V.; PRELL, W. & RUDDIMAN, W.F. (1976): Glacial North Atlantic 18,000 years ago: a CLIMAP reconstruction. – In: CLINE, R.M. & HAYES, J.D. (Eds.): Geological Society of America, Memoir 145, pp 43-74.

MEHLUM, F. (1989): Summer distribution of Seabirds in northern Greenland and the Barents Sea. – Norsk Polarinstitutt Skrifter 191. 56 pp.

MEHLUM, F. (1990): Seabird distribution in the northern Barents Sea marginal ice-zone during the summer. – Polar Research 8: 61-65.

MEHLUM, F.; HUNT G.L.jr.,; DECKER, M.B. & NORDLUND, N. (1998): Hydrographic Features, Cetaceans and the Foraging of Thick-Billed Murres and Other Marine Birds in the Northwestern Barents Sea. – Arctic Vol. 51, No. 3: 243-252.

MEINCKE, J. (1983): The modern current regime across the Greenland-Scotland ridge. – In: BOTT, M.H.; SAXOV, S.; TALWANI, M. & THIE, J.H. (Eds.): Structure and development of the Greenland-Scotland ridge. – (Plenum Press) New York, pp 637-650.

MELNIKOV, I.A. (1989): Ecosystem of the Arctic sea ice. – Inst. Oceanol., Acad. Sci. Moscow, USSR (in Russian).

MELNIKOV, I.A. (1997): The Arctic sea ice ecosystem. – (Gordon and Breach science publishers) Amsterdam, 204 pp.

MENZIES, R.J. (1962): The isopods of the abyssal depths of the Atlantic Ocean. – Vema Research Series 1: 79-206.

MENZIES, R.J. (1963): The abyssal fauna of the floor of the Artic Ocean. – In: Proceedings of the Arctic Basin Symposium, 1962. – Arctic Institute of North America, Washington DC, pp 46-66.

MENZIES, R.J. (1975): Origin and evolution of the Arctic marine ecosystem. – In: Proceedings of the Circumpolar Conference in Northern Ecology (September 15-18). – National Research Council of Canada, Ottawa, pp II/15–II/25.

MENZIES, R.J.; GEORGE, R.Y. & ROWE, G.T. (1973): Abyssal Environment and Ecology of the World Oceans. – (John Wiley & Sons) New York, 488 pp.

MERRETT, N.R. (1986): Biogeography and the oceanic rim: A poorly known zone of ichtyofaunal interaction. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, pp 201-209.

MERRETT, N.R. (1987): A zone of faunal change in assemblages of abyssal demersal fish in the eastern North Atlantic: a response to seasonality in production? – Biological Oceanography 5: 137-151.

MERRETT, N.R. & HAEDRICH, R.L. (1997): Deep-Sea demersal fish and fisheries. – (Chapman & Hall) London, 282 pp.

MICHANEK, G. (1979): Phytogeographic provinces and seaweed distribution. – Botanica marina 22: 375-391.

MICHANEK, G. (1983): World resources of marine plants. – In: KINNE, O. (Ed.): Marine Ecology, Vol. V, Part 2 – (John Wiley) New York, pp 795-837.

MIDTTUN, L. (1985): Formation of dense bottom water in the Barents Sea. – Deep-Sea Research 32(10): 1233-1241.

MIDTTUN, L. & LOENG, H. (1987): Climatic variations in the Barents Sea. – In: LOENG, H. (Ed.): The effect of oceanographic conditions on distribution and population dynamics of commercial fish stocks in the Barents Sea. – Proceedings of the third Soviet-Norwegian symposium, Murmansk, 26-28 May 1986. Institute of Marine Research, Bergen, pp 13-27.

MITCHELL, R. (1987): Conservation of marine benthic biocenoses in the North Sea and the Baltic. A framework for the establishment of an European network of marine protected areas in the North Sea and the Baltic. – Strasbourg, Council of Europe for European Committee for the Conservation of Nature and Natural Resources. (Nature and Environment Series, No. 37. (Conservation des biocénoses marines benthiques de la mer du Nord et de la Baltique. Conseil de l'Europe, Strasbourg.)

MITCHELL, R.; EARLL, R.C. & DIPPER, F.A. (1983): Shallow sublittoral ecosystems in the Inner Hebrides. – In: BOYD, J.M. & BOWES, D.R. (Eds.): Proceedings of the Royal Society of Edinburgh. Series B: Biological Sciences 83: 161-184.

MITTELSTAEDT, E. (1991): The ocean boundary along the northwest African coast: circulation and oceanographic properties at the sea surface. – Progress in Oceanography 26(4): 307-355.
MONNIOT, F. (1979): Faunal affinities among abyssal Atlantic basins. – Sarsia 64: 93-95.
MONNIOT, C. & MONNIOT, F. (1975): Abyssal tunicates: an ecological paradox. – Annales de l'Institute Océanographique, Paris 51: 99-129.
MONNIOT, C. & MONNIOT, F. (1990): Relationships between deep-sea tunicate populations west and east of the Straits of Gibraltar. – Progress in Oceanography 24: 289-296.
MORGAN, J.R. (1987): Large Marine Ecosystems an emerging concept of regional management. – Environment 29(10): 4-9 & 29-34.
MORTENSEN, P. B.; HOVLAND, M.; BRATTEGARD, T. & FARESTVEIT, R. (1995): Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64 ° N on the Norwegian shelf: structure and associated megafauna. – Sarsia 80: 145-158.
MÜHLDORFER, H. & LUTTER, S. (Eds.) (1998): flyer: "WWF's North-East Atlantic Programme". – WWF's North-East Atlantic Programme Coordination Office, Bremen.
MULLER, P.J. (1979): Introduccion a la Zoogeografi. (editión en castellano). – (Ed. Blume) Barcelona.
MÜLLER, P. (1980): Biogeographie. – (Eugen Ulmer Verlag) Stuttgart.
MÜLLER, P. (1981): Arealsysteme und Biogeographie. – (Eugen Ulmer Verlag) Stuttgart.
MULLINEAUX, L.; JUNIPER, S.K. & DESBRUYÈRES, D. (1998): Deep-Sea Sanctuaries at Hydrothermal Vents: A Position Paper. – InterRidge News 7(1): 15-16.
NEGOESCU, I. & SVAVARSSON, J. (1997): Anthurideans (Crustacea, Isopoda) from the North Atlantic and the Arctic Ocean. – Sarsia 82:159-202.
NELSON, G. (1986): Models and Prospects of historical Biogeography. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, pp 214-218.
NELSON, G. & D.E. ROSEN (Eds.) (1981): Vicariance Biogeography: A Critique. – (Columbia University Press) New York.
NEUMANN, G. (1968): Ocean currents. – (Elsevier) Amsterdam, London, New York, 352 pp.
NEWTON, A. & ROWE, G. (1995): The abundance of benthic calcareous Foraminifera and other meiofauna at a time series station in the Northeast Water Polynya, Greenland. – Journal of Geophysical Research 100: 4423-4438.
NICOLAS, A. (1995): The Mid-Oceanic Ridges. Mountains below sea level. – (Springer) Berlin, 200 pp.
NIEBAUER, H.J. & ALEXANDER, V. (1985): Oceanographic frontal structure and biological production at an ice-edge. – Continental Shelf Research 4: 367-388.
NIJKAMP, H.; JOORDENS, J.C.A. & VAN BRUMMELEN, T.C. (1998): Marine ecological network to conserve and restore biodiversity in the OSPAR maritime area. – OSPAR Workshop on Marine Protected Areas, Vilm 31. 8.– 4.9.1998, papers presented by the Netherlands.
NYBAKKEN, J.W. (1997): Marine Biology. An Ecological Approach. (4th edn.). – (Addison Wesley Longman) Menlo Park, CA, USA.
OKOLODKOV, Y.B. & DODGE, J.D. (1996): Biodiversity and biogeography of planktonic dinoflagellates in the Arctic Ocean. – Journal of Experimental Marine Biology and Ecology 202: 19-27.
ÓLAFSSON, J.; HONJO, S.; THORS, K.; STEFÁNSSON, U.; JONES, R.R. & BALLARD, R.D. (1989): Initial observations, bathymetry and photography of a geothermal site on the Kolbeinsey Ridge. – In: AYALA-CASTAÑAREA, A.; WOOSTER, W. & YÀÑEZ-ARANCIBIA, A. (Eds.): Oceanography 1988. – (UNAM Press) Mexico, pp 208.
OLSON, D.B. & HOOD, R.R. (1994): Modelling pelagic biogeography. – In: ANGEL, M.V. & SMITH, R.L. (Eds.) Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 161-205.
OLSON, D.M. & DINERSTEIN, E. (1998): The Global 200: A representation approach to conserving the earth's distinctive ecoregions. – Conservation Science Program, World Wildlife Fund-US, Washington.

OMORI, M.; VAN DER SPOEL, S. & NORMAN, C.P. (1994): Impact of human activities on pelagic biogeography. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 211-219.

ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V. (Eds.) (1997): Marine biodiversity: Patterns and processes. – (Cambridge University Press) Cambridge, UK, 449 pp.

ORTMANN, A. (1896): Grundzüge der marinen Tiergeographie. – (Gustav Fischer Verlag) Jena, 96 pp.

OSPAR – ASMO (14.-18.3.1994): Description of the Regions. Annex 5 (Ref.§ 6.7). Dresden, D.

OSPAR – ASMO (7.-11.4.1997): Editorial changes to the description of the Regions of the maritime area. 1.6 Description of the Regions of the Maritime Area. Annex 15 (Ref.§ 3.14a). Copenhagen, DK.

OWEN, R.W. (1981): Fronts and Eddies in the Sea: Mechanisms, Interactions and Biological Effects. – In: OWEN, R.W. (Ed.): Fronts and Eddies in the Sea. – (Academic Press) London, UK, pp 197-233.

PALMISANO, A.C. & SULLIVAN, C.W. (1985): Growth, Metabolism, and Dark Survival in Sea Ice Microalgae. – In: HORNER, R.A. (Ed.): Sea Ice Biota. – (CRC Press) Boca Raton, Florida, pp 131-146.

PARIN, N.V. (1984): Oceanic ichtyogeography: an attempt to review the distribution and origin of pelagic and bottom fishes outside continental shelves and neritic zones. – Arch. Fisch. Wiss. 35: 5-41.

PARIN, N.V. (1986): Distribution of mesopelagic fishes in slope waters and around submarine rises. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, pp 226-229.

PARSON, L.M.; WALKER, C.L. & DIXON, D.R. (Eds.) (1995): Hydrothermal Vents and Processes. – Geological Society Special Publication No. 87, Geological Society of London.

PATERSON, G.L.J.; WILSON, G.D.F.; COSSON, N. & LAMONT, P.A. (1998): Hessler and Jumars (1974) revisited: abyssal polychaete assemblages from the Atlantic and Pacific. – Deep-Sea Research II 45: 225-251.

PATTERSON, C. (1983): Aims and Methods in Biogeography. – In: SIMS, R.W.; PRICE, J.H. & WHALLEY, P.E.S. (Eds.): Evolution, Time and Space: The Emergence of the Biosphere. – The Systematics Association Special Volume No. 23. – (Academic Press) London, pp 1-28.

PAUL, A.Z. & MENZIES, R.J. (1974): Benthic ecology of the high Arctic deep-sea. – Marine Biology 27(3): 251-262.

PEDERSEN, R.B. & SUNDVOR, E. (1998): Manned submersible dives to the Knipovich Ridge, Norwegian-Greenland Sea. – InterRidge News 7.2.

PEET, G.; NIJKAMP, H.; ROSSUM, J.; SLEGTENHORST, C.; BUS, M.; NOLKAEMPER, A. & GUBBAY, S. (Eds.) (1993): Marine protected areas in Europe. MPA descriptions. – Report of a study within the framework of the BioMar projekt (3 vols.). LIFE92-1/IRL/00 1.

PÉRÈS, J. (1957): Le probleme de étagement des formations benthiques. – In: Recueil des Travaux de la Station Marine d'Endoume, Bulletin 21(12) – Université d'Aix-Marseille, Faculté des Sciences, pp 4-21.

PÉRÈS, J. M. (1982): Specific pelagic assemblages. – In: KINNE, O. (Ed.): Marine Ecology. Volume V, Part 1 – (John Wiley) New York, pp 313-522.

PETERSEN, G.H. & CURTIS, M.A. (1980): Differences in energy flow through major components of subarctic, temperate and tropical marine shelf ecosystems. – Dana 1: 53-64.

PICTON, B.E. & COSTELLO, M. J. (1998): The BioMar biotope viewer: a guide to marine habitats, fauna and flora in Britain and Ireland. – Environmental Sciences Unit, Trinity College, Dublin.

PIELOU, E.C. (1977): The latitudinal spans of seaweed species and their pattern of overlap. – Journal of Biogeography 4: 299-311.

PIELOU, E.C. (1978): Latitudinal overlap of seaweed species: evidence for quasi-sympatric speciation. – Journal of Biogeography 5: 227-238.

PIELOU, E.C. (1979): Biogeography. – (Wiley-Interscience) New York, NY, USA, 351 pp.

PIEPENBURG, D. (1988a): Absolute densities and spatial distribution patterns of epibenthic species from Fram Strait. – Rapports et Procès-Verbaux des Réunions. Conseil Internationale pour l'Exploration de la Mer 188: 180.

PIEPENBURG, D. (1988b): Zur Zusammensetzung der Bodenfauna in der westlichen Fram-Straße. – Berichte zur Polarforschung 52: 1-118.

PIEPENBURG, D.; AMBROSE, W.G. jr.; BRANDT, A.; RENAUD, P.E.; AHRENS, M.J. & JENSEN, P. (1997): Benthic community patterns reflect water column processes in the Northeast Water polynya (Greenland). – Journal of Marine Systems 10 (1-4): 467-482.

PIERROT-BULTS, A.C. (1975): Taxonomy and zoogeography of *Sagitta planctonis* Steinhaus 1896 (Chaetognata) in the Atlantic Ocean. – Beaufortia 23: 27-51.

PIERROT-BULTS, A.C. (1997): Biological diversity in oceanic macrozooplankton: More than counting species. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V. (Eds.): Marine Biodiversity. Patterns and Processes. – (Cambridge University Press) Cambridge, pp 69-93.

PIERROT-BULTS, A.C. & VAN DER SPOEL, S. (1979): Speciation in macrozooplankton. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 144-167,

PIERROT-BULTS, A.C.; VAN DER SPOEL, S., ; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.) (1986): Pelagic biogeography. – Proceedings of an international conference The Netherlands 29 May-5 June 1985. – UNESCO technical papers in marine science no. 49, Paris, 295 pp.

PINEDA, J. (1993): Boundary effects on the vertical ranges of the deep-sea benthic species. – Deep-Sea Research 40: 2179-2192.

PINEDA, J. & CASWELL, H. (1998): Bathymetric species-diversity patterns and boundary constraints on vertical range distributions. – Deep-Sea Research II 45: 83-101.

PINGREE, R.D. (1978): Mixing and stabilization of phytoplankton distributions on the northwest European shelf. – In: STEELE, J.H. (Ed.): Spatial Patterns in Plankton Communities. – (Plenum Press) New York, pp 181-220.

PINGREE, R.D. (1993): Flow of surface waters to the west of the British Isles and in the Bay of Biscay. – Deep-Sea Research 40: 369-388.

PINGREE, R.D. & GRIFFITHS, D.K. (1978): Tidal fronts on the shelf sea areas around the British Isles. – Journal of Geophysical Research 83: 4615-4622.

PINGREE, R.D.; FORSTER, G.R. & MORRISON, G.K. (1974): Turbulent convergent tidal fronts. – Journal of the Marine Biological Association of the United Kingdom 54: 469-479.

PINGREE, R.D.; HOLLIGAN, P.M.; MARDELL, G.T. & HEAD, R.N. (1976): The influence of physical stability on spring, summer, and autumn phytoplankton blooms in the Celtic Sea. – Journal of the Marine Biological Association of the United Kingdom 56: 845-873.

PINGREE, R.D.; PUGH, P.R.; HOLLIGAN, P.M. & FORSTER, G.R. (1975): Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. – Nature (London) 258: 672-677.

PINGREE, R.D. & LE CANN, B. (1990): Structure, strength and seasonality of the slope currents in the Bay of Biscay region. – Journal of the Marine Biological Association of the United Kingdom 70: 857-885.

PLATTS, E. (1985): An annotated list of of the North Atlantic Opistobranchia. – Ophelia Supplement 2: 150-170.

POLTERMANN, M. (1997): Biologische und ökologische Untersuchungen zur kryopelagischen Amphipodenfauna des arktischen Meereises. – Berichte zur Polarforschung 225, Bremerhaven, 170 pp.

POR, F.D. (1978): Lessepsian Migration: the influx of Red Sea biota into the Mediterranean. – (Springer) Berlin.

PRESCOTT, J.R.V. (1989): The political division of large marine ecosystems in the Atlantic Ocean and some associated seas. – In: SHERMAN, K. & ALEXANDER, L.M. (Eds.): Biomass yields and geography of large marine ecosystems. – AAAS Selected Symposium 111, – (Westview Press) Boulder, pp 395-442.

PRICE, A. & HUMPHREY, S. (1993): Application of the biosphere concept to coastal marine areas. A Marine Conservation and Development Report. Papers presented at the UNESCO/IUCN San Francisco Workshop of 14-20 August, 1989. Gland, Switzerland: IUCN.

PRICE, J.H. (1967): The distribution of benthic marine algae. A bibliography for the British Isles, – Supplement 1. British Phycological Journal 3: 305-315.

PRICE, J.H. & W.F. FARNHAM (1982): Seaweeds of Faroes. 3. Open shores. – Bulletin of the British Museum for Natural History, Botany Series 10: 153-225.
PRICE, J.H. & I. TITTLEY (1970): The distribution of benthic marine algae. A bibliography for the British Isles, – Suppl. 2. British Phycological Journal 5: 103-112.
PRICE, J.H. & I. TITTLEY (1975): The distribution of benthic marine algae. A bibliography for the British Isles, – Supplement 3. British Phycological Journal 10: 299-307.
PRUD'HOMME VAN REINE, W.F. (1988): Phytogeography of seaweeds of the Azores. Helgoländer Meeresuntersuchungen 42: 165-185, Hamburg.
PRUD'HOMME VAN REINE, W.F. & VAN DEN HOEK, C. (1988): Biogeography of the Cape Verdean seaweeds. – Courier Forsch.-Inst. Senckenberg 105: 35-49.
PRUD'HOMME VAN REINE, W.F. & VAN DEN HOEK, C. (1990): Biogeography of Macaronesian seaweeds. – Courier Forsch.-Inst. Senckenberg 129: 55-73.
PUGH, P.R. (1984): The diel migrations and distributions within a mesopelagic community in the Northeast Atlantic: 7.Siphonophores. – Progress in Oceanography 13: 461-489.
RAFFI, S. (1986): The significance of marine boreal molluscs in the early Pleistocene fauna of the Mediterranean Sea. – Palaeogeography, Palaeoclimatology, Palaeoecology 52: 267-289.
RAFFI, S.; STANLEY, M. & MARASTI, R. (1985): Biogeographic patterns and Plio-Pleistocene extinction of Bivalvia in the Mediterranean and southern North Sea. – Palaeogeography, Palaeoclimatology, Palaeoecology 11: 368-388.
RÄTZ, H.-J. (1984): Qualitative und quantitative Untersuchungen der Ichtyozönose in der archibenthischen Zone des Rockall-Grabens und umliegender Bänke (Westbritische Gewässer). – Mitteilungen aus dem Institut für Seefischerei (34): 152 pp.
RASS, T.S. (1986): Vicariance ichtyogeography of the Atlantic Ocean Pelagial. – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. – Proceedings of an International Conference The Netherlands, 29 May-5 June 1985. – UNESCO Technical Papers in Marine Science No. 49, Paris, pp 237-241.
RAY, E.C. (1976): Geography of phocid evolution. – Systematic Zoology 25: 391-406.
RAY, G.C. (1975): A Preliminary Classification of Coastal and Marine Environments. – IUCN Occasional Paper No. 14, IUCN, Morges, Switzerland. 26 pp.
RAY, G.C. (1988): Ecological diversity in coastal zones and oceans. – In: WILSON, E.O. (Ed.): Biodiversity. – (National Academic Press) Washington DC, USA, pp 36-50.
RAY, G.C. (1991): Coastal-zone biodiversity patterns. – BioScience 41: 490-498.
RAY, G.C.; CLARK, J.R.; FOSTER, N.M.; GODFREY, P.; HAYDEN, B.P.; LEATHERMAN, S.P.; ODUM, W.E.; SATHER, J.H. & GREGG, W.P. jr. (1981): Interim Guidelines for Identification and Selection of Coastal Biosphere Reserves. – United States Man and the Biosphere Program (MAB-8), US MAB Rep. No. 6, 33 pp.
RAY, G.C.; HAYDEN, B. & DOLAN, R. (1982): Development of a Biophysical Coastal and Marine Classification System. – In: MCNEELY, J.A. & MILLER, K.R. (Eds.): National Parks, Conservation, and Development: The Role of Protected Areas in Sustaining Society. (Proceedings of the World National Parks Congress, Bali, Indonesia, 1982.) – Smithsonian Institution Press, Washington DC, USA.
RAY, G.C. & MCCORMICK-RAY, M.G. (1987): Coastal and Marine Biosphere Reserves. – In: Symposium on Biosphere Reserves, Fourth World Wilderness Congress, US National Parks Service, pp 68-78.
RAY, G.C. & HAYDEN, B.P. (1990): Marine biogeographic provinces of the Bering, Chukchi and Beaufort Seas. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large marine ecosystems: patterns, processes and yields. – American Association for the Advancement of Science, Washington DC, USA, pp 175-184.
RAY, G.C. & HAYDEN, B.P. (1992): Coastal zone ecotones. – In: HANSEN, A.J. & DI CASTRI, F. (Eds.) Landscape boundaries. – (Springer) New York, pp 403-420.
REES, E.I.S. & HOPE-JONES, P. (1982): Seabirds associated with frontal systems in the Irish Sea. – In: HOPE-JONES, P. (Ed.): Proceedings of the Seabird Group Conference 12-14. February, 1982. Nature Conservancy Council.

REES, H.L.; PENDLE, M.A.; WLADOCK, R.; LINPENNY, D.S. & BOYD, S.E. (1999): A comparison of benthic biodiversity in the North Sea, English Channel and Celtic Seas. – ICES Journal of Marine Science 56: 228-246.

REINERT, J. (1995): Deep water resources in Faroese waters to the south, southwest and west of the Faroes – a preliminary account. – In: HOPPER, A.G. (Ed.) (1995): Deep-Water Fisheries of the North Atlantic Oceanic Slope. – Nato Advanced Science Institutes Series E–Vol 296. – (Kluwer Academic Publishers) Dordrecht, pp 201-225.

REISE, K. & BARTSCH, I. (1990): Inshore and offshore diversity of epibenthos dredged in the North Sea. – Netherlands Journal of Sea Research 25: 175-179.

REMMERT, H. (1980): Arctic animal ecology. – (Springer) Berlin, Heidelberg, New York.

RENARD, V. & MASCLE, J. (1974): Eastern Atlantic Continental Margins: Various Structural and Morphological Types. – In: BURK, C.A. & DRAKE, C.L. (Eds.): The Geology of Continental Margins. – (Springer) Berlin, pp 285-291.

REPENNING, C.A.; RAY, C.E. & GRIGORESCU, D. (1979): Pinniped biogeography. – In: GRAY, J. & BOUCOT, A.J. (Eds.): Historical Biogeography, Plate Tectonics and the Changing Environment. – (Oregon State University Press) Corvallis, Oregon, pp 357-369.

REX, M.A. (1977): Zonation in deep-sea gastropods: The importance of biological interactions to rates of zonation. – In: KEEGAN, B.F.; CEIDIGH, P.Ó. & BOADEN, P.J.S. (Eds.): Biology of Benthic Organisms. – 11th European Symposium on Marine Biology, Galway, October 1976. – (Pergamon Press) New York, Oxford, pp 521-530.

REX, M.A. (1981): Community structure in the deep-sea benthos. – Annual Review of Ecology and Systematics 12: 331-353.

REX, M.A. (1983): Geographic patterns of species diversity in the deep-sea benthos. – In: ROWE, G.T. (Ed.): Deep-Sea Biology. The Sea, Vol. 8. – (John Wiley and Sons) New York, pp 453-472.

REX, M.A.; ETTER, R.J. & STUART, C.T. (1997): Large-scale patterns of species diversity in the deep-sea benthos. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V.: Marine Biodiversity. Patterns and Processes. – (Cambridge University Press), Cambridge, pp 94-121.

REX, M.A.; STUART, C.T.; HESSLER, RR.; ALLEN, J.A.; SANDERS, H.L. & WILSON, G.D.F. (1993): Global scale latitudinal patterns of species diversity in the deep-sea benthos. – Nature (London) 365: 636-639.

REY, F. & LOENG, H. (1985): The influence of ice and hydrographic conditions on the development of phytoplankton in the Barents Sea. – In: GRAY, J.S. & CHRISTIANSEN, M.E. (Eds.): Marine biology of polar regions and effects of stress on marine organisms. – Proceedings of the 18th European Marine Biology Symposium, Oslo, Norway, 14-20 August 1983. – (John Wiley & Sons) Chichester, pp 49-63.

RICE, A.L.; THURSTON, M.H. & BETT, B.J. (1994): The IOSDL DEEPSEAS programme: introduction and photographic evidence for the presence and absence of a seasonal input of phytodetritus at contrasting abyssal sites in the north-eastern Atlantic. – Deep-Sea Research I 41: 1305-1320.

RICHTER, D. (1992): Allgemeine Geologie. 4. Edn. – (de Gruyter) Berlin.

RIDGEWAY,S.H. & HARRISON, R.J. (Eds.) (1981 a): Handbook of Marine Mammals, Vol. 1. The Walrus, Sea Lions, Fur Seals and Sea Otter. – (Academic Press) London, 235 pp.

RIDGEWAY,S.H. & HARRISON, R.J. (Eds.) (1981 b): Handbook of Marine Mammals, Vol. 2. Seals. – (Academic Press) London, 359 pp.

RIDGEWAY,S.H. & HARRISON, R.J. (Eds.) (1985): Handbook of Marine Mammals, Vol. 3. The Sirenians and Baleen Whales. – (Academic Press) London, 362 pp.

RIDGEWAY,S.H. & HARRISON, R.J. (Eds.) (1989): Handbook of Marine Mammals, Vol. 4. River Dolphins and the larger Toothed Whales. – (Academic Press) London, 442 pp.

RIDGWAY, S.H. & HARRISON, R.J. (Eds.) (1994): Handbook of Marine Mammals. Vol. 5, The First Book of Dolphins. – (Academic Press) London, New York, 416 pp.

RIDGWAY, S.H. & HARRISON, R.J. (Eds.) (1998): Handbook of Marine Mammals. Vol. 6, The Second Book of Dolphins and Porpoises. – (Academic Press) London, New York, 465 pp.

ROBERTS, D.G. (1974): Structural Development of the British Isles, the Continental Margin, and the Rockall Plateau. – In: BURK, C.A. & DRAKE, C.L. (Eds.): The Geology of Continental Margins. – (Springer) Berlin, pp 343-359.

ROBERTS, M. (1997): Coral in deep waters. – New Scientist, 20 September 1997.
ROBINSON, M.K.; BAUER, R.A. & SCHROEDER, E.H. (1979): Atlas of the north Atlantic-Pacific Ocean monthly mean temperatures and mean salinities of the surface layer. – U.S. Naval Oceanographic Science Report 225.
RODEN, G.I. (1987): Effect of seamount chains on ocean circulation and thermohaline structure. – In: KEATING, B.H.; FRYER, P.; BATIZA, R. & BOEHLERT, G.W. (Eds.): Seamounts, islands, and atolls. – Geophysical monograph 43, American Geophysical Union, Washington DC, pp 335-354.
ROE, H.S.J. (1985): The diel migrations and distributions within a mesopelagic community in the Northeast Atlantic: 2. Vertical migrations and feeding in mysids and decapod Crustacea. – Progress in Oceanography 13: 269-318.
ROE, H.S.J. (1984): The diel migrations and distributions within a mesopelagic community in the Northeast Atlantic: 4.The copepods. – Progress in Oceanography 13: 353-388.
ROFF, J.C. & TAYLOR, M.E. (2000): Viewpoint: National frameworks for marine conservation - a hierarchical geophysical approach. – Aquatic Conservation: Marine and Freshwater Ecosystems 10: 209-223.
ROGERS, A.D. (1994): The biology of seamounts. – Advances in Marine Biology 30: 305-350.
ROGERS, A.D. (1999): The biology of *Lophelia pertusa* [Linnaeus 1758] and other deep-water reef-forming corals and impacts from human activities. – International Review of Hydrobiology 84(4): 315-406.
ROUX, M. (1985): Les Crinoïds pédonculés (Echinoderms) de l'Atlantique N.E.: Inventaire, Écologie et Biogéographie. – In: LAUBIER, L. & MONNIOT, C. (Eds.): Peuplements profonds du Golfe de Gascogne: Campagnes BIOGAS. – (IFREMER, Service Documentation-Publications) Brest, France, pp 479-489.
ROWE, G.T. (1971): Benthic biomass and surface productivity. – In: COSTLOW, J.D. jr. (Ed.): Fertility of the Sea. – (Gordon and Breach Science) New York, pp. 441-454.
ROWE, G.T. (Ed.) (1983): Deep-Sea Biology. The Sea, Vol. 8 – (John Wiley and Sons) New York, 560 pp.
ROWE, G.T. (1983): Biomass and production of the deep-sea macrobenthos. – In: ROWE, G.T. (Ed.): Deep-Sea Biology. The Sea, Vol. 8 – (John Wiley and Sons) New York, pp 97-121.
ROWE, G.T. (1996): The cycling of organic matter in food-limited environments. – In: UIBLEIN, F.; OTT, J. & STACHOWITSCH, M. (Eds.): Deep sea and extreme shallow-water habitats: affinities and adaptions. Biosystematics and Ecology Series 11. – Österreichische Akademie der Wissenschaften, Wien, pp 233-260.
ROWE, G.T. & R. MENZIES (1969): Zonation of large benthic invertebrates in the deep-sea off the Carolinas. – Deep-Sea Research 16: 531-581.
ROWE, G.T.; POLLONI, P. & HAEDRICH, R.L. (1982): The deep-sea macrobenthos on the continental margin of the northwest Atlantic Ocean. – Deep-Sea Research 29A: 257-278.
SAKSHAUG, E. & SKJOLDAL, H.R. (1989): Life at the ice edge. – Ambio 18: 60-67.
SAKSHAUG, E.; BJØRGE, A.; GULLIKSEN, B.; LOENG, H. & MEHLUM, F. (1994): Structure, biomass distribution, and energetic of the pelagic ecosystem in the Barents Sea: A synopsis. – Polar Biology 14: 405-411.
SALDANHA, L.; BISCOITO, M. & DESBRUYÈRES, D. (1996): The Azoran deep-sea hydrothermal ecosystem: Its recent discovery. – In: UIBLEIN, F.; OTT, J. & STACHOWITSCH, M. (Eds.): Deep sea and extreme shallow-water habitats: affinities and adaptions. — Österreichische Akademie der Wissenschaften, Wien – Biosystematics and Ecology Series 11: pp 383-388.
SALM, R.V. & CLARK, J. (1984): Marine and coastal protected areas: A guide for planners and managers. – IUCN, Gland, Switzerland.
SALM, R. & PRICE, A. (1995): Selection of marine protected areas. – In: GUBBAY, S. (Ed.): Marine Protected Areas - Principles and Techniques for Management. – (Chapman and Hall) London.
SALOMONSEN, F. (1972): Zoogeographical and ecological studies in Arctic birds. – Proc. 15th Int. Ornithol. Congr. 25-77.
SALZWEDEL, H.; RACHOR, E.& GERDES, D. (1985): Benthic macrofauna communities in the German Bight. – Veröffentlichungen des Institut für Meeresforschung in Bremerhaven 20: 199-267.

SANTOS, R.S. (2000): Habitat classification proposal for Azores Triple Junction hydrothermal vents. Discussion paper prepared for the 2nd OSPAR/ICES/EEA workshop on habitat classification, Southampton/England, 18-22.9.2000.

SANTOS, R.S.; HAWKINS, S.; MONTEIRO, L.R.; ALVES, M. & ISIDRO, E.I. (1995): Marine research, resources and conservation in the Azores. – Aquatic Conservation: Marine and Freshwater Ecosystems 5: 311-354.

SARNTHEIN, M. & ALTENBACH, A.V. (1995): Late Quaternary changes in surface water and deep water masses of the Nordic Seas and north-eastern North Atlantic: a review. – Geologische Rundschau 84: 89-107.

SARNTHEIN, M.; WINN, K.; JUNG, S.J.A.; DUPLESSY, J.C.; LABEYRIE, L.; ERLENKEUSER, H. & GANSSEN, G. (1994): Changes in East Atlantic deep water circulation over the last 30,000 years: an eight time slice record. – Paleoceanography 9: 209-267.

SAUVAGEAU, C. (1897): Note préliminaire sur les algues marines du golfe de Gascogne. – Journal de Botanique 11: 166-307.

SCHÄFER, P.; THIEDE, J.; GERLACH, S.; GRAF, G. & ZEITZSCHEL, B. (1995): Global environmental change: the northern North Atlantic. – Geologische Rundschau 84: 3-10.

SCHEIN-FATTON, E. (1988): Relations between the bathymetric range of Pectinidae (Bivalvia) and their dispersal in the deep sea (Abstract). Fifth Deep-Sea Biology symposium, June 26th-July 1st 1988 – Institut Français de Recherche pour L'Exploitation de la Mer (IFREMER), Brest.

SCHENK, H.G. & KEEN, M.A. (1937): An index-method for comparing molluscan faunules. – Proceedings of the American Philosophical Society, Vol. 77, No. 2: 162-168.

SCHENK, H.G. & KEEN, M.A. (1940): Biomerical analysis of molluscan assemblages. – Mémoires de la Société de Biogéographie, Vol. 7: 379-392.

SCHILDER, F.A. (1956): Lehrbuch der Allgemeinen Zoogeographie. – (VEB Gustav Fischer Verlag) Jena.

SCHMIDT, O.C. (1931): Die marine Vegetation der Azoren in ihren Grundzügen dargestellt. – Bibliotheka bot. 102: 1-116 + 10 plates, Stuttgart.

SCHNEIDER, W. & BUDÉUS, G. (1994): The north east water polynya. – Polar Biology 14:1-9.

SCHNEIDER, W. & BUDÉUS, G. (1995): On the generation of the Northeast water Polynya. – Journal of Geopysical Research, Vol. 100, No. C3: 4269-4286.

SCHNEIDER, W. & BUDÉUS, G. (1997): Summary of the Northeast water Polynya formation and development (Greenland Sea). – Journal of Marine Systems 10: 107-122.

SCHOLTEN, J. et al. (1999): Hydrothermal activity along the Tjoernes Fracture Zone, north of Iceland: Initial results of R/V Poseidon cruises 252 and 253. – InterRidge News 8.2.

SCHOPF, T.J.M.; FISHER, J.B. & SMITH, C.A.F. (1978): Is the marine latitudinal diversity gradient merely another example of the species area curve? – In: BATTAGLIA, B. & BEARDMORE, J.A. (Eds.): Marine Organisms: Genetics, Ecology and Evolution. Plenum Press, New York, pp 365-386.

SCHOTT, G. (1942): Geographie des Atlantischen Ozeans. – (C. Boysen) Hamburg, 438 pp.

SCHULTZ, J. (1995): The ecozones of the world, the ecological divisions of the geosphere. – (Springer) Berlin, Germany.

SCHWARTZ, M.L. (1982): The encyclopedia of beaches and coastal environments. – (Hutchinson Ross Publishing Company) Philadelphia, Pennsylvania.

SCLATER, J.G. & TAPSCOTT, C. (1979): The history of the Atlantic. – Scientific American 240: 120-132.

SCLATER, J.G.; HELLINGER, S. & TAPSCOTT, C. (1979): The paleobathymetry of the Atlantic Ocean from the Jurassic to the present. – The Journal of Geology, Vol. 85, No 5: 509-552.

SCLATER, P.L. (1885): On the General Geographical Distribution of the Members of the Class Aves. – Journal of the Linnean Society (Zool.) 2: 130-145.

SCOR (Scientific Commitee on Oceanic Research) WORKING GROUP 76 (1994): Suggested criteria for describing deep-sea benthic communities; the final report of SCOR Working Group 76. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 81-100.

SEIBOLD, E. & BERGER, W.H. (1993): The Sea Floor. – (Springer) Berlin, 356 pp.

SEMINA, H.J. (1997): An outline of the geographical distribution of oceanic phytoplankton. – In: GEBRUK, A.; SOUTHWARD, E. & TAYLOR, P. (Eds.): The Biogeography of the Oceans. – Advances in Marine Biology, Vol. 32, (Academic Press) San Diego, pp 527-563.

SETCHELL, W.A. (1917): Geographical distribution of the marine algae. – Science 45: 197-204.
SHERMAN, K. (1993): Large Marine Ecosystems as Global Units for Marine Resources Management – An Ecological Perspective. – In: SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.): Large Marine Ecosystems. Stress, Mitigation, and Sustainability. – AAAS Washington DC, USA, pp 3-14.
SHERMAN, K. (1994): Sustainability, biomass yields, and health of coastal ecosystems: an ecological perspective. – Marine Ecology Progress Series 112: 277-301.
SHERMAN, K. & ALEXANDER, L.M. (Eds.) (1986): Variability and management of large marine ecosystems. – AAAS Selected Symposium 99 –(Westview Press) Boulder. 319 pp.
SHERMAN, K. & ALEXANDER, L.M. (Eds.) (1989): Biomass yields and geography of large marine ecosystems. – AAAS Selected Symposium 111 – (Westview Press) Boulder, 493 pp.
SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.) (1990): Large Marine Ecosystems. Patterns, Processes, and Yields. – AAAS, Washington DC, USA.
SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.) (1991): Food chains, yields, models, and management of large marine ecosystems. – AAAS Symposium – (Westview Press) Boulder, 320 pp.
SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.) (1992): Large marine ecosystems: patterns, processes and yields. – American Association for the Advancement of Science/AAAS, Washington DC, USA.
SHERMAN, K.; ALEXANDER, L.M. & GOLD, B.D. (Eds.) (1993): Large Marine Ecosystems. Stress, Mitigation, and Sustainability. – AAAS. Washington DC, USA.
SHERMAN, K. & BUSCH, D.A. (1995): Assessment and monitoring of large marine ecosystems. – In: RAPPORT, D.J.; GUADET, C.L. & CALOW, P. (Eds.): Evaluating and monitoring the health of large scale ecosystems. – (Springer) Berlin. (Published in cooperation with NATO Scientific Affairs Division). – NATO Advanced Science Institute Series. Series 1: Global Environmental Change, Vol. 28, pp 385-430.
SHERMAN, K.; LASKER, R.; RICHARDS, W. & KENDALL, A.W. (1983): Ichtyoplankton and fish recruitment studies in large marine ecosystems. – Mar. Fish. Rev. 45: 1-25.
SHERMAN, K. & LAUGHLIN, T. (1992): The large marine ecosystem (LME) concept and its application to regional marine resources management. – Marine Conservation Development Reports. IUCN, Gland, Switzerland.
SIBUET, M. (1977): Répartition et diversité des echinoderms (holothurides – astérides) en zone profonde dans le Golfe de Gascogne. – Deep-Sea Research 24: 549-563.
SIBUET, M. (1979): Distribution and Diversity of Asteroids in Atlantic Abyssal Basins. – Sarsia 64(1-2): 85-91.
SIBUET, M. (1985): Quantitative distribution of echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, Echinoidea) in relation to organic matter in the sediment, in deep-sea basins of the Atlantic Ocean. – In: KEEGAN, B.F.& O'CONNOR, B.D.S. (Eds.): Echinodermata. – (Balkema) Rotterdam, pp 99-108.
SIBUET, M. & OLU, K. (1998): Biogeography, biodiversity and fluid dependence of deep-sea cold-seep communities at active and passive margins. – Deep-Sea Research II 45: 517-567.
SIMS, R.W.; PRICE, J.H. & WHALLEY, P.E.S. (Eds.) (1983): Evolution, Time and Space: The Emergence of the Biosphere. – The Systematics Association Special Volume No. 23, (Academic Press) London.
SIMPSON, J.H.; ALLEN, C.M. & N.C.G. MORRIS (1978): Fronts on the continental shelf. – Journal of Geophysical Research 83, No. C9: 4607-4614.
SIMPSON, J.H.; D.G. HUGHES & MORRIS, N.C.G. (1977): The relation of seasonal stratification to tidal mixing on the continental shelf. – In: ANGEL, M.: A voyage of discovery. – (Pergamon Press) Oxford, pp 327-340.
SIMPSON, J.H. (1981): The shelf-sea fronts: implications of their existence and behaviour. – Philosophical Transactions of the Royal Society of London. Series A, Vol. 302: 531-546.
SKJOLDAL, H.R. & REY, F. (1989): Pelagic production and variability of the Barents Sea ecosystem. – In: SHERMAN, K. & ALEXANDER, L.M. (Eds.): Biomass yields and geography of large marine ecosystems. – AAAS Selected Symposium 111, (Westview Press) Boulder, Colorado, USA, pp 242-286.
SMITH, C.R.; LEVIN, L.A. & MULLINEAUX, L.S. (1998): Deep-sea biodiversity: a tribute to Robert R. Hessler. – Deep-Sea Research II 45: 1-11.

SMITH, J.E. & RISK, M.J.; SCHWARCZ, H.P. & MCCONNAUGHEY, T.A. (1997): Rapid climate change in the North Atlantic during the younger Dryas recorded by deep-sea corals. – Nature (London) 386: 818-820.

SMITH, S.L.; SMITH, W.O.; CODISPOTI, L.A. & WILSON, D.L. (1990): Biological observations in the ice zone of the east Greenland Sea. Journal of Marine Research 43: 693-717.

SMITH, S.D.; MUENCH, R.D. & PEASE, C.H. (1990): Polynyas and leads: An overview of physical processes and environment. – Journal of Geophysical Research 95: 9461-9479.

SMITH W.O. jr. (1987): Phytoplankton dynamics in marginal ice zones. – Oceanography and Marine Biology: Annual Review 25: 11-38.

SMITH, W.O. jr. (1995): Primary productivity and new production in the Northeast Water (Greenland) Polynya during summer 1992. – Journal of Geophysical Research 100(C3): 4357-4370.

SMITH, W.O. jr.; WALSH, I.D.; BOOTH, B.C. & DEMING, J.W. (1995): Particulate matter and phytoplankton and bacterial biomass distributions in the Northeast Water Polynya during summer 1992. – Journal of Geophysical Research 100(C3): .

SOKOLOVA, M.N. (1997): Trophic structure of abyssal macrobenthos. – In: GEBRUK, A.; SOUTHWARD, E. & TAYLOR, P. (Eds.): The Biogeography of the Oceans. – Advances in Marine Biology, Vol 32. (Academic Press) San Diego, pp 427-525.

SOKOLOVA, M.N. (2000): Feeding and Trophic Structure of the Deep-Sea Macrobenthos. – (Smithsonian Institution Library) Washington D.C.; (Amerind Publishing Co.) New Dehli, 264 pp.

SOMERS, E. (1995): Legal Constraints and Options for Total Ecosystem Management of Large Marine Ecosystems. – In: OKEMWA, E.; NTIBA, M.J. & SHERMAN, K. (Eds.): A Report of the International Symposium and Workshop. – A Marine Conservation and Development Report. IUCN, Gland, Switzerland, pp 27-34.

SOURNIA, A. (1994): Pelagic biogeography and fronts. – IN: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 109-120.

SOURNIA, A.; CHRÉTIENNOT-DINET, M.-J. & RICARD, M. (1991): Marine phytoplankton: How many species in the worls ocean? – Journal of Plankton Research 13: 1093-1099.

SOUTH, G.R. & TITTLEY, I. (1986): A checklist and distributional index of the benthic marine algae of the North Atlantic ocean. – Huntsman Marine Laboratory and British Museum (Nat. Hist.), St. Andrews & London, 76 pp.

SOUTHWARD, A.J. (1958): Notes on the temperature tolerances of some intertidal animals in relation to environmental temperatures and geographical distribution. – Journal of the Marine Biological Association of the United Kingdom 37: 49-66.

SOUTHWARD, A.J. (1980): The Western English Channel – an inconstant ecosystem? – Nature (London) 285: 361-366.

SOUTHWARD, A.J. & CRISP, D.J. (1954): The distribution of certain intertidal animals around the Irish coast. – Proc. R. Irish Acad. Vol. 57 (B), No.1, 29 pp.

SOUTHWARD, A.J. & CRISP, D.J. (1956): Fluctuations in the distribution of and abundance of intertidal barnacles. – Journal of the Marine Biological Association of the United Kingdom 35: 211-229.

SOUTHWARD, E.C. (1979): Horizontal and vertical distribution of Pogonophora in the Atlantic Ocean. – Sarsia 64: 51-55.

SOUTHWARD, E.C. (1985): Pogonophora. – In: LAUBIER, L. & MONNIOT, C. (Eds.): Peuplements profonds du Golfe de Gascogne: Campagnes BIOGAS. – (IFREMER, Service Documentation-Publications) Brest, France, pp 369-373.

SOUTHWARD, E.C. & SOUTHWARD, A.J. (1967): The distribution of Pogonophora in the Atlantic Ocean. – Symposia of the Zoological Society of London 19: 145-158.

SPINDLER, M. (1990): A comparison of Arctic and Antarctic sea ice and the effects of different properties on sea ice biota. – In: BLEIL, U. & THIEDE, J.: Geological history of the polar oceans: Arctic versus Antarctic. – (Kluwer Academic Publishers) The Netherlands, pp 173-186.

STARMANS, A. (1997): Comparative studies on the ecology and biodiversity of the Arctic and Antarctic mega-epibenthos. – Berichte zur Polarforschung 250, Bremerhaven. 150 pp.

STEELE, J.H. (1974): The Structure of Marine Ecosystems. – (Blackwell Scientific Publications) Oxford and (Harvard University Press) Cambridge, MA.

STEELE, J.H. (1975): Marine climate and the biogeography of the surface waters in the northwest Atlantic. – Naturaliste Canadien. 102: 189-198.
STEELE, J.H. (Ed.) (1978): Spatial Patterns in Plankton Communities. – (Plenum Press) New York.
STEELE, J.H. (1991): Marine functional diversity. – BioScience 41: 470-474.
STEFÁNSSON, U. (1962): North Icelandic waters. – Rit Fiskideildar 3: 1-269.
STEFÁNSSON, U. (1969): Sjávarhiti á siglingaleið umhverfis Ísland. – In: EINARSSON, M.Á. (Ed.): Hafisinn. – (Almenna Bókafélagið) Reykjavik, pp 131-149.
STEFÁNSSON, U. & GUÐMUNDSSON, A. (1969): Hydrographic conditions off the northeast coast of Iceland in relation to meteorological factors. – Tellus 11(2): 245-258.
STIRLING, I. (1997): The importance of polynyas, ice edges, and leads to marine mammals and birds. – In: HIRCHE, H.-J. & DEMING, J.W. (Eds.): Northeast Water Polynya Symposium. – Journal of Marine Systems 10 (1-4): 9-21.
SUCHANEK, T.H. (1994): Temperate coastal marine communities: Biodiversity and threats. – American Zoologist 34:100-114.
SUNDVOR, E. (1997): Joint U.S., Russian and Norwegian research at Knipovich Ridge, Norwegian-Greenland Sea. – InterRidge News 6.1.
SVAVARSSON, J. (1987): Systematics and zoogeography of arctic deep sea asellote isopods (Crustacea, Isopoda), with notes on the biology of the eurycopid *Eurycope brevirostris* Hansen, 1916 (Asellota, Eurycopidae), Göteborgs Universitet (Dissertation).
SVAVARSSON, J. (1997): Diversity of isopods (Crustacea): new data from the Arctic and Atlantic Oceans. – Biodiversity and Conservation 6: 1571-1579.
SVAVARSSON, J. (1999): The deep water gnathiid *Caecognathia bicolor* (Hansen, 1916) (Crustacea, Isopoda, Gnathiidae) - redescription and new data on its distribution. – Rit Fiskideildar 16: 171-185.
SVAVARSSON, J.; BRATTEGARD, T. & STRÖMBERG, J.-Ö. (1990): Distribution and diversity patterns of asellote isopods (Crustacea) in the deep Norwegian and Greenland Seas. – Progress in Oceanography 24: 297-310.
SVAVARSSON, J.; STRÖMBERG, J.-Ö. & BRATTEGARD, T. (1993): The deep-sea asellote (Isopoda, Crustacea) fauna of the Northern Seas: species composition, distributional patterns and origin. – Journal of Biogeography 20(5): 537-555.
SVEDELIUS, N. (1924): On the discontinuous geographical distribution of some tropical and subtropical marine algae. – Arkiv. Bot. 19: 1-70.
SVERDRUP, H.U.; JOHNSON, M.W. & FLEMING, R.H. (1942 [1946]): Animals in Relation to Physical-Chemical Properties of the Environment. Chapter 17 – In: SVERDRUP, H.U.; JOHNSON, M.W. & FLEMING, R.H.: The oceans, their physics, chemistry, and general biology. – (Prentice-Hall Inc.) New York [Englewood], pp 799-878.
SVERDRUP, H.U.; JOHNSON, M.W. & FLEMING, R.H. (1942 [1946]): The oceans, their physics, chemistry, and general biology. – (Prentice-Hall Inc.) New York [Englewood].
SWIFT, J.H. (1986): The Arctic waters. – In: HURDLE, B.G. (Ed.): The Nordic Seas. – (Springer) Berlin, pp 129-153.
SWIFT, J.H.; AARGAARD, K. & MALMBERG, S.-A. (1980): The contribution of the Denmark Strait overflow to the deep North Atlantic. – Deep-Sea Research 27: 29-42.
SWIFT, J.H.; TAKAHASHI, T. & LIVINGSTON, H.D. (1983): The contribution of the Greenland and Barents seas to the deep water of the Arctic Ocean. – Journal of Geophysical Research 88: 5981-5986.
TAMBS-LYCHE, H. (1958): Zoogeographical and Faunistic Studies on West Norwegian Marine Animals. – Universitetet i Bergen. Årbok 1958. Naturvitenskapelig rekke Nr. 7. – (A.S. John Griegs Boktrykkeri) Bergen, 24 pp.
TARLING, D.H. (1982): Land bridges and plate tectonics. – Mémoir Spéciale Géobios 6: 361-374.
TAYLOR, J.D. & TAYLOR, C.N. (1977): Latitudinal distribution of predatory gastropods on the eastern Atlantic shelf. – Journal of Biogeography 4: 73-81.
TENCATI, J.R. & GEIGER, S.R. (1968): Pelagic amphipods of the slope waters of northeast Greenland. – Journal of the Fisheries Research Board of Canada 25: 1637-1650.
THE NATURE CONSERVANCY (1997): Designing a geography of hope: Guidelines for ecoregion-based conservation. – In: The Nature Conservancy, Arlington, Virginia, USA, 77 pp.

THIEDE, J. (1980): Paleo-oceanography, margin stratigraphy and paleophysiography of the Tertiary North Atlantic and Norwegian-Greenland Seas. – Philosophical Transactions of the Royal Society of London. Series A, Vol. 294: 177-185.

THIEDE, J.; ELDHOLM, O. & TAYLOR, E. (1989): Variability of Cenozoic Norwegian-Greenland Sea paleooceanography and northern hemisphere paleoclimate. – In: ELDHOLM, O.; THIEDE, J. & TAYLOR, E., et al.: Proceedings of the Ocean Drilling Program, Scientific Results Vol. 104. – College Station, Texas, pp 1067-1118.

THIEDE, J.; CLARK, D.L. & HERMAN, Y. (1990): Late Mesozoic and Cenozoic paleoceanography of Northern Polar Oceans. – In: GRANTZ, A.; JOHNSON, L. & SWEENEY, J.F. (Eds.): The Geology of North America, Vol.L., The Arctic Ocean region. – The Geological Society of America, Boulder, Colorado, pp 427-458.

THIEL, H. (1972): Meiofauna und Struktur der benthischen Lebensgemeinschaften des Iberischen Tiefseeboden. – Meteor Forschungen Ergebnisse, Reihe D 12: 36-51.

THIEL, H. (1983): Meiobenthos and Nanobenthos of the deep sea. – In: ROWE, G.T. (Ed.): Deep-Sea Biology. The Sea, Vol. 8 – (John Wiley and Sons) New York, pp 167-230.

THIEL, H. (1992): Deep-sea environmental disturbance and recovery potential. – Internationale Revue der gesamten Hydrobiologie 77(2): 331-119.

THIEL, H. & KOSLOW, T. (1999): Do we need oceanic MPAs? – Ocean Challenge 9(2): 14-15

THIEL, H.; PFANNKUCHE, O.; SCHREIVER, G.; LOCHTE, K.; GOODAY, A.J.; HEMLEBEN, C.H.; MANTOURA, R.F.G.; TURLEY, C.M.; PATCHING, J.W. & RIEMANN, F. (1989): Phytodetritus on the deep-sea floor in a central oceanic region of the Northeast Atlantic. – Biological Oceanography 6: 203-239.

THIEL, H.; PÖRTNER, O. & ARNTZ, W.E. (1996): Marine life at low temperatures–a comparison of polar and deep-sea characteristics. – In: UIBLEIN, F.; OTT, J. & STACHOWITSCH, M. (Eds.): Deep sea and extreme shallow-water habitats: affinities and adaptions. – Biosystematics and Ecology Series 11. Österreichische Akademie der Wissenschaften, Wien, pp 183-219.

THORSETH, I.H.; TORSVIK, T.; FURNES, H. & MUEHLENBACHS, K. (1995): Microbes play an important role in the alteration of oceanic crust. – Chemical Geology 126(2): 137-146.

THORSON, G. (1941): Marine Gastropoda Prosobranchiata. – Zoology of Iceland 4: 1-15.

THORSON, G. (1944): The Zoology of East Greenland. Marine Gastropoda Prosobranchiata. – Meddelelser om Grønland 121: 1-181.

THORSON, G. (1957): Bottom communities (sublittoral or shallow shelf). – Memoirs of the Geological Society of America 67: 461-534.

THORSON, G. (1971): Life in the sea. – World University Library. – (McGraw-Hill) New York.

THUNELL, R. & BELYEA, P. (1982): Neogene planktonic foraminiferal biogeography of the Atlantic Ocean. – Micropaleontology 28: 381-398.

THURSTON, M.H. (1979): Scavenging abyssal amphipods from the north-east Atlantic Ocean. – Marine Biology 51: 55-68.

THURSTON, M.H. (1990): Abyssal necrophagous amphipods (Crustacea: Amphipoda) in the northeast and tropical Atlantic Ocean. – Progress in Oceanography 24: 257-274.

THURSTON, M.H.; BETT, B.J.; RICE, A.L. & JACKSON, P.A.B. (1994): Variations in the invertebrate abyssal megafauna in the North Atlantic Ocean. – Deep-Sea Research I, 41: 1321-1348.

THURSTON, M.H.; BETT, B.J. & RICE, A.L. (1995): Abyssal necrophagous amphipods in the Eastern North Atlantic Ocean. – Internationale Revue der gesamten Hydrobiologie, Volume 80, No. 2: 267-286.

THURSTON, M.H.; RICE, A.L. & BETT, B.J. (1998): Latitudinal variation in invertebrate megafaunal abundance and biomass in the North Atlantic Ocean Abyss. – Deep-Sea Research II 45: 203-224.

TICKELL, C. (1997): The value of Diversity. – In: ORMOND, R.F.G.; GAGE, J.D. & ANGEL, M.V.: Marine Biodiversity, Patterns and Processes. – (Cambridge University Press) Cambridge, pp 13-22.

TITTLEY, I.; FARNHAM, W.F. & GRAY, P.G.W. (1982): Seaweeds of the Faroes. 2. Sheltered fjords and sounds. – Bulletin of the British Museum of Natural History, Botany Series 10: 133-151.

TITTLEY, I.; FARNHAM, W.F.; FLETCHER, R.L.; MORELL, S. & BISHOP, G. (1985): Sublittoral seaweed assemblages of some northern Atlantic islands. – Progress in Underwater Science 10: 39-52.

TITTLEY, I.; PATERSON, G.L.J.; LAMBSHEAD, P.J.D. & SOUTH, G.R. (1989): Algal provinces in the North Atlantic - Do they exist? – In: GARBARY, D.J. & SOUTH, G.R. (Eds.): Evolutionary biogeogeography of the marine algae of the North Atlantic. – (Springer) Berlin, pp 291-322.

TITTLEY, I. & A.I. NETO (1994): Marine algae collected during "Expedition Azores 1989", with discussion of biogeography. – Arquipélago, Life and Marine Sciences 12A: 1-13.

TOKIOKA, T. (1979): Neritic and oceanic plankton. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, pp 126-143.

TROYANOVSKY, F.M. & LISOVSKY, S.F. (1995): Russian (USSR) fisheries research in deep waters (below 500 m) in the North Atlantic. – In: HOPPER, A.G. (Ed.): Deep-Water Fisheries of the North Atlantic Oceanic Slope. – Nato Advanced Science Institutes Series E, Vol. 296 – (Kluwer Academic Publishers) Dordrecht, pp 357-365.

TUNNICLIFFE, V.; MCARTHUR, A.G. & MCHUGH, D. (1998): A biogeographical perspective of the deep-sea hydrothermal vent fauna. – (Academic Press) San Diego, Advances in Marine Biology 34: pp 353-442.

TÜRKAY, M. (1982): Marine Crustacea Decapoda von den Capverdischen Inseln mit Bemerkungen zur Zoogeographie des Gebietes. – Courier Forsch.-Inst. Senckenberg 52: 91-129.

TYLER, P.A. (1988): Seasonality in the deep sea. – Oceanography and Marine Biology; an Annual Review 26: 227-258.

TYLER, P.A. (1995): Conditions for life at the deep-sea floor: an update. – Oceanography and Marine Biology: an Annual Review 33: 221-224.

TYLER, P.A. (1996): Faunal responses to temporal disequilibrium in the deep sea. – In: UIBLEIN, F.; OTT, J. & STACHOWITSCH, M. (Eds.): Deep sea and extreme shallow-water habitats: affinities and adaptions. – Biosystematics and Ecology Series 11. Österreichische Akademie der Wissenschaften, Wien, pp 261-270.

UNITED NATIONS (1983): The Law of the Sea: Official text of the United Nations Convention on the Law of the Sea (with annexes and index). – United Nations, New York, Publication E.83 v.5,224 pp.

UDVARDY, M.D.F. (1975): A Classification of the Biogeographical Provinces of the World. – IUCN Occasional Paper No. 18, IUCN, Morges, Switzerland. 49 pp.

VALENTINE, J.W. (1973): Evolutionary Paleoecology of the Marine Biosphere. – (Prentice Hall) Englewood Cliffs, N.Y.

VALENTINE, J.W. & JABLONSKI, D. (1983): Speciation in the Shallow Sea: General Patterns and Biogeographic Control. – In: SIMS, R.W.; PRICE, J.H. & WHALLEY, P.E.S. (Eds.): Evolution, Time and Space: The Emergence of the Biosphere. – The Systematics Association Special Volume No. 23. – (Academic Press) London, pp 201-226.

VALENTINE, J.W. & MOORES, E.M. (1974): Plate tectonics and the history of life in the oceans. – Scientific American 230(4): 80-89.

VAN ANDEL, T.H. (1979): An eclectic overview of plate tectonics, paleogeograohy, paleoecology. – In: GRAY, J. & BOUCOT, A.J. (Eds.): Historical Biogeography, Plate Tectonics and the Changing Environment. – (Oregon State University Press) Corvallis, Oregon, pp 9-25.

VAN CAMP, L.; NYKJÆR, L.; MITTELSTAEDT, E. & SCHLITTENHARDT, P. (1991): Upwelling and boundary circulation off Northwest Africa as depicted by infrared and visible satellite observations. – Progress in Oceanography 26(4): 357-402.

VAN DEN HOEK, C. (1975): Phytogeographic provinces along the coasts of the northern Atlantic Ocean. – Phycologia 14: 317-330.

VAN DEN HOEK, C. (1979): The phytogeography of Cladophora (Chlorophyceae) in the northern Atlantic Ocean, in comparison to that of other benthic algal species. – Helgoländer Meeresuntersuchungen 32: 374-393.

VAN DEN HOEK, C. (1982a): Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. – Helgoländer Meeresuntersuchungen 35: 153-214.

VAN DEN HOEK, C. (1982b): The distribution of benthic marine algae in relation to the temperature regulation of their life histories. – Biological Journal of the Linnean Society 18: 81-144.

VAN DEN HOEK, C. (1982c): A taxonomic revision of the American species of Cladophora (Chlorophyceae) in the North Atlantic Ocean and their geographic distribution. – (North-Holland

Publishing Company) Amsterdam. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen. Afdeling Natuurkunde 2de Reeks 78: 1-236.

VAN DEN HOEK, C. (1984): World-wide longitudinal seaweed distribution patterns and their possible causes, as illustrated by the distribution of rhodophytan genera. – Helgoländer Meeresuntersuchungen 38: 227-257.

VAN DEN HOEK, C. (1987): The possible significance of long-range dispersal for the biogeography of seaweeds. – Helgoländer Meeresuntersuchungen 41: 261-272.

VAN DEN HOEK, C. & BREEMAN, A.M. (1989): Seaweed biogeography of the North Atlantic: where are we now?– In: GARBARY, D.J. & SOUTH, G.R.: Evolutionary biogeography of the marine algae of the North Atlantic. – (Springer) Berlin, pp 58-86.

VAN DEN HOEK, C.; BREEMAN, A.M. & STAM, W.T. (1990): The geographic distribution of Seaweed species in relation to temperature: present and past. – In: BEUKEMA, J.J. et al. (Eds.): Expected effects of Climatic Change on Marine Coastal Ecosystems. – Developments in Hydrobiology 57. Kluwer Academic Publishers, Dordrecht, pp 55-67.

VAN DEN HOEK, C. & DONZE, M. (1966): The algal vegetation on the rocky Côte Basque (SW France). – Bulletin du Centre d'Études et de Recherches Scientifiques de Biarritz 6(2): 289-319.

VAN DEN HOEK, C. & DONZE, M. (1967): Algal phytogeography of the European Atlantic coasts. – Blumea 15: 63-89.

VAN DER SPOEL, S. (1983): Patterns in plankton distribution and their relation to speciation: the dawn of pelagic biogeography. – In: SIMS, R.W.; PRICE, J.H. & WHALLEY, P.E.S. (Eds.): Evolution, Time and Space: The Emergence of the Biosphere. – The Systematics Association Special Volume No. 23. – (Academic Press) London, pp 291-334.

VAN DER SPOEL, S. (1986): What is unique about open-ocean biogeography; zooplankton? – In: PIERROT-BULTS, A.C.; VAN DER SPOEL, S.; ZAHURANEC, B.J. & JOHNSON, R.K. (Eds.): Pelagic biogeography. Proceedings of an international conference The Netherlands, 29 May-5 June 1985. – UNESCO Technical Papers in Marine Science No. 49, Paris, pp 254-260.

VAN DER SPOEL, S. (1994 a): History, progress and future of theory in pelagic biogeography. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 101-107.

VAN DER SPOEL, S. (1994 b): The basis for boundaries in pelagic biogeography. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 121-133.

VAN DER SPOEL, S. (1994 c): A warning from the deep. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 207-210.

VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.) (1979): Zoogeography and diversity of plankton. – (Arnold) London & (Bunge) Utrecht, 410 pp.

VAN DER SPOEL, S. & HEYMAN, R.P. (1983): A comparative atlas of zooplankton. – (Bunge) Utrecht, 186 pp.

VAN DER SPOEL, S.; PIERROT-BULTS, A.C. & SCHALK, P.H. (1990): Probable mesozoic vicariance in the biogeography of Euphausiacea. – Bijdragen tot de Dierkunde 60: 155-162.

VAN DOVER, C.L. (1995): Ecology of Mid-Atlantic Ridge hydrothermal vents. – In: PARSON, L.M.; WALKER, C.L. & DIXON, D.R. (Eds.): Hydrothermal Vents and Processes. – Geological Society Special Publication No. 87, Geological Society of London, pp 257-293.

VANREUSEL, A.; VINCX, M.; BETT, B.J. & RICE, A.L. (1995): Nematode Biomass Spectra at Two Abyssal Sites in the NE Atlantic with a Contrasting Food Supply. – Internationale Revue der gesamten Hydrobiologie, Vol. 80, No. 2: 287-296.

VAN SOEST, R.W.M. (1979): North-South diversity. – In: VAN DER SPOEL, S. & PIERROT-BULTS, A.C. (Eds.): Zoogeography and diversity of plankton. (Arnold) London & (Bunge) Utrecht, pp 103-111.

VARELA, M. (1992): Upwelling and phytoplankton ecology in Galician (NW Spain) rías and shelf waters. – Boletin del Instituto Espanol de Oceanografia 8: 57-74.

VAUGHAN, T.W. (1940): Ecology of modern marine organisms with reference to paleogeography. – Bulletin of the Geological Society of America, Vol. 51: 433-468.

VERMEIJ, G.J. (1978): Biogeography and adaptation. Patterns of marine life. – (Harvard University Press) Cambridge, Mass., 332 pp.
VERMEIJ, G.J. (1989): Geographical restriction as a guide to the causes of extinction: the case of the cold northern oceans during the Neogene. – Paleobiology 15: 335-356.
VERMEIJ, G.J. (1991): Anatomy of an invasion: the trans-Arctic interchange. – Paleobiology 17(3): 281-307.
VERMEIJ, G.J. (1992): Trans-equatorial connections between biotas in the temperate eastern Atlantic. – Marine Biology 112: 343-348.
VERMEIJ, G.J. (1996): Marine Biological Diversity: Muricid Gastropods as a Case Study. – In: JABLONSKI, D.; ERWIN, D.H. & LIPPS, J.H. (Eds.): Evolutionary Paleobiology. In honor James W. Valentine. – (University of Chicago Press) Chicago and London, pp 355-375.
VIGNEAUX, M. (1974): The Geology and Sedimentation History of the Bay of Biscay. – In: NAIRN, A.E.M. & STELHI, F.G. (Eds.): The ocean basins and margins. Vol. 2: The North Atlantic. – (Plenum Press) New York, pp 273-314.
VINJE, T. (1980): On the extreme sea ice conditions observed in the Greenland and Barents seas in 1979. – Norsk Polarinstitutt Årbok.
VINJE, T. (1985): Drift, composition, morphology and distribution of the sea ice fields in the Barents Sea. – Norsk Polarinstitutt Skrifter 179C, p 26.
VINJE, T. & KVAMBEKK, Å.S. (1991): Barents Sea drift ice characteristics. – Polar Research 10: 59-68.
VINJE, T.; NORDLUND, N. & KVAMBEKK, Å.S. (1998): Monitoring ice thickness in Fram Strait. – Journal of Geophysical Research 103(C5): 10437-10449.
VINOGRADOV, M.E. (1961): The feeding of deep-sea zooplankton. – In: FRASER, J.H. & CORLETT, J.: Rapports et Procès-Verbaux des Réunions. Conseil Internationale pour l'Exploration de la Mer 153: 114-120.
VINOGRADOV, M.E. (1968): Vertical distribution of the Oceanic Zooplankton. – Akademiya Nauk SSSR, Institut Okeanologii, Academy of Sciences of the USSR, Institute of Oceanography. – English translation in: "Israel Program for ScientificTranslation" series, Jerusalem (1970), 339 pp.
VINOGRADOV, M.E. (1997): Some Problems of Vertical Distribution of Meso- and Macroplankton in the Ocean. – In: GEBRUK, A.; SOUTHWARD, E. & TAYLOR, P. (Eds.): The Biogeography of the Oceans. – (Academic Press) San Diego – Advances in Marine Biology, Vol. 32, pp 1-92.
VINOGRADOVA, N.G. (1956): Zoogeographical subdivision of the abyssal of the World Ocean. – Doklady Akademii Nauk SSSR 111: 195-198 (in Russian).
VINOGRADOVA, N.G. (1959): The zoogeographical distribution of the deep-water bottom fauna in the abyssal zone of the ocean. – Deep-Sea Research 5: 205-8.
VINOGRADOVA, N.G. (1962): Vertical zonation in the distribution of the deep-sea benthic fauna in the ocean. – Deep-Sea Research 8: 245-250.
VINOGRADOVA, N.G. (1969a): The vertical distribution of the deep-sea bottom fauna. – In: KORT, V.G. (Ed.): The Pacific Ocean. Biology of the Ocean, Book 2. The Deep-Sea Bottom Fauna, Pleuston. – (Izd-vo'Nauka') Moscow (in Russian), pp 125-153.
VINOGRADOVA, N.G. (1969b): The geographical distribution of the deep-sea bottom hauls. – In: KORT, V.G. (Ed.): The Pacific Ocean. Biology of the Ocean, Book 2. The Deep-Sea Bottom Fauna, Pleuston. – (Izd-vo'Nauka') Moscow (in Russian), pp 154-181.
VINOGRADOVA, N.G. (1979): The geographical distribution of the abyssal and hadal (ultraabyssal) fauna in relation of the vertical zonation of the ocean. – Sarsia 64: 41-50.
VINOGRADOVA, N.G. (1997): Zoogeography of the abyssal and hadal zones. – In: GEBRUK, A.; SOUTHWARD, E. & TAYLOR, P. (Eds.): The Biogeography of the Oceans. – Advances in Marine Biology, Vol. 32. – (Academic Press) San Diego, pp 325-387.
VINOGRADOVA, N.G. & ZEZINA, O.N. (1998): Zoogeographic regions (benthic fauna). – In: HÖLZEL, Ed. (Ed.): Resources and Environment World Atlas, Part II. Institute of Geography – (Russian Academy of Science/IG RAS), Moscow & (Ed. HÖLZEL) Vienna, p 109.
VOGT, P.R. & AVERY, O.E. (1974): Tectonic History of the Arctic Basins: Partial Solutions and Unsolved Mysteries. – In: HERMAN, Y. (Ed.) Marine Geology and Oceanography of the Arctic Seas. – (Springer) Berlin, pp 83-118.

VOGT, P.R.; CHERKASHEV, G.; GINSBURG, G.; IVANOV, G.; CRANE, K.; EGOROV, A.; LEIN, A.; PIMENOV, N. & SUNDVOR, E. (1997): Proceedings of the American Geophysical Union Spring Meeting, May 27-30, 1997; Ocean Sciences. Geobiology of Critical Intervals: High-Latitude Gas Venting, Hydrates, and Mass Wasting Posters. – Baltimore, Maryland.

VON BODUNGEN, B.; ANTIA, A.; BAUERFEIND, E.; HAUPT, O.; KOEVE, W.; MACHADO, E.; PEEKEN, I.; PEINERT, R.; REITMEIER, S.; THOMSEN, C.; VOSS, M.; WUNSCH, M.; ZELLER, U. & ZEITSCHEL, B. (1995): Pelagic processes and vertical flux of particles: an overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. – Geologische Rundschau 84: 11-27.

WADHAMS, P.; GILL, A.E.; & LINDEN, P.F. (1979): Transects by submarine of the East Greenland Polar Front. – Deep Sea Research 26(12A): 1311-1327.

WARNER, A.J. & HAYS, G.C. (1994): Sampling by the Continuous Plankton Recorder Survey. – In: ANGEL, M.V. & SMITH, R.L. (Eds.); Scientific commitee on oceanic research: Ecology of the deep sea floor and pelagic biogeography. – Progress in Oceanography 34(2-3): 237-256.

WARWICK R.; GONI, R. & HEIP, C. (Eds.) (1997): An inventory of marine biodiversity projects in the EU/EEA member states. – MARS, Netherlands Institute of Ecology, Yerseke.

WCMC (1996): Biodiversity map library. Digital database. – World Conservation Monitoring Centre, Cambridge, UK.

WEISSHAPPEL, J.B.F. & SVAVARSSON, J. (1998): Benthic amphipods (Crustacea, Malacostraca) in Icelandic waters: diversity in relation to faunal patterns from shallow to intermediate deep Arctic and North Atlantic Oceans. – Marine Biology 131:133-143.

WESTERBERG, H. (1979): Benthic temperatures in the Faroe area. – Department of Oceanography, University of Gothenburg, Report No. 51. ISSN 0349-0122.

WHITEHEAD, P.J.P.; BAUCHOT, M.L.; HUREAU, J.C.; NIELSEN, J. & TORTONESE, E. (Eds.) (1984-86): Fishes of the north-eastern Atlantic and the Mediterranean (FNAM). – Vols. I-III. UNESCO, Paris: Vol. I (1984): 1-510; Vol. II (1986): 517-1007; Vol. III (1986): 1015-1473.

WHEELER, A. (1969): The fishes of the British Isles and North-west Europe. – (Macmillan) London.

WHEELER, A. (1978): Key to the fishes of northern Europe: a guide to the identification of more than 350 species. – (Warne) London.

WILCE, R.T. (1989): Role of the Arctic Ocean as a bridge between the Atlantic and Pacific Oceans: Facts and Hypothesis. – In: GARBARY, D.J. & SOUTH, G.R.: Evolutionary biogeography of the marine algae of the North Atlantic. – (Springer) Berlin, pp 323-347.

WILSON, J.B. (1979a): The distribution of the coral *Lophelia pertusa* (L.) in the North-East Atlantic. – Journal of the Marine Biological Association of the United Kingdom 59: 149-164.

WILSON, J.B. (1979b): 'Patch' development of the deep-water coral *Lophelia pertusa* (L.) on Rockall Bank. – Journal of the Marine Biological Association of the United Kingdom 59: 165-177.

WILSON, R.R. & KAUFMANN, R.S. (1987): Seamount biota and biogeography. – In: KEATING, B.H.; FRYER, P.; BATIZA, R. & BOEHLERT, G.W. (Eds.): Seamounts, islands, and atolls. – Geophysical Monograph 43, American Geophysical Union, Washington DC., pp 355-377.

WMO (WOLRD METEOROLOGICAL ORGANIZATION) (1970): WMO sea-ice nomenclature. – WMO/OMM/BMO No 259.TP.145, Geneva.

WOLFF, T. (1977): Diversity and faunal composition of the deep-sea benthos. – Nature (London) 267: 780-785.

WOLFF, T. (Ed.); BRUUN, A.F.; GREVE, S.V. & SPÄRCK, R. (ed. commitee) (1961): Galathea Report, Vol. 4. – (Danish Science Press LTD.) Copenhagen.

WOLFF, W.J. (1983): The Ecology of the Wadden Sea. – (Balkema) Rotterdam.

WOOD, E. (1988): Sea life of Britain and Ireland. – (Immel) London.

WOODWARD, S.P. (1856): A manual of the Mollusca: A treatise on recent and fossil shells. 1st edn. – (Virtue Brothers) London. (2nd edn. 1866) (4th edn. 1880: Crosby Lockwood and Co., London).

WOOSTER, W.S.; BAKUN, A. & MCLAIN, D.R. (1976): The seasonal upwelling cycle along the eastern boundary of the North Atlantic. – Journal of Marine Research 34(2): 131-141.

WORTHINGTON, L.V. (1976): On the North Atlantic circulation. The Johns Hopkins Oceanographic Studies, Vol. 6. – (Johns Hopkins University Press) Baltimore, U.S.A., 110 pp.

WWF (2000): Developing a Framework for Marine Protected Areas in the North-East Atlantic. Report from the Workshop held 13-14 November 1999 in Brest, France. – WWF International, North-East Atlantic Programme, Bremen, Germany.

WYATT, T. & LARRAÑETA, M.G. (Eds.) (1988): Long term changes in marine fish populations: a symposium in Vigo, España, 18-21 November, 1986. – (Imprenta Real.) Vigo. 554 pp.

WYATT, T. & PEREZ-GANDARAS, G. (1989): Biomass changes in the Iberian ecosystem. – In: SHERMAN, K. & ALEXANDER, L.M. (Eds.): Biomass yields and geography of large marine ecosystems. – AAAS Selected Symposium 111. – (Westview Press) Boulder, CO, pp 221-239.

YARISH, C.; BREEMANN, A.M. & VAN DEN HOEK, C. (1984): Temperature, light, and photoperiod responses of some Northeast American and West European endemic rhodophytes in relation to their geographic distribution. – Helgoländer Meeresuntersuchungen 38: 273-304, Hamburg.

YARISH, C.; BREEMANN, A.M. & VAN DEN HOEK, C. (1986): Survival strategies and temperature responses of seaweeds belonging to different biogeographic distribution groups. – Berlin & New York – Botanica Marina 29: 215-230.

ZENKEVITCH, L. (1933): Beiträge zur Zoogeographie des nördlichen Polarbassins im Zusammenhang mit der Frage über dessen paläogeographische Vergangenheit. – Zoological Journal Vol. 12, No. 4.

ZENKEVITCH, L. (1948): Biologicheskaya structura okeana (Biological structure of the ocean). Zoologicheski Zhurnal 27(2): 113-124 (in Russian with English abstract). – Or: C. R. 13 Congrès Inter. Zool (1949): La structure biologique de l'ocean. pp 522-529.

ZENKEVITCH, L. (1963): Biology of the Seas of the U.S.S.R. (translated by S. Botcharska). – (George Allen and Unwin Ltd.) London, 955 pp.

ZEZINA, O.N. (1997): Biogeography of the bathyal zone. – In: GEBRUK, A.; SOUTHWARD, E. & TAYLOR, P. (Eds.): The Biogeography of the Oceans. – Advances in Marine Biology, Vol. 32. – (Academic Press) San Diego, pp 389-426.

ZIBROWIUS, H. (1980): Les Scléractiniares de la Méditerranée et de l'Atlantique nord-oriental. – Mémoires de l'Institut Océanographique, Monaco 11: 1-284.

Lieferbare* Veröffentlichungen des Bundesamtes für Naturschutz

*Das kostenlose **Gesamtverzeichnis** kann beim Landwirtschaftsverlag bzw. beim BfN angefordert werden. Außerdem ist es im Internet unter der Adresse: www.lv-h.de/bfn abrufbar.

Schriftenreihe für Landschaftspflege und Naturschutz

Heft 1: Der Landschaftsplan – Inhalt, Methodik, Anwendungsbereiche.
Hochwasserbedingte Landschaftsschäden im Einzugsgebiet der Altenau und ihrer Nebenbäche.
1966. 190 S. ISBN 3-7843-2001-5

Heft 2: I. Aktuelle Rechtsfragen des Naturschutzes. II. Gutachten über das Naturschutzgebiet „Lister Dünen mit Halbinsel Ellenbogen auf Sylt".
1967. 114 S. ISBN 3-7843-2002-3

Heft 3: Beiträge zur Neuordnung des ländlichen Raumes. Wettbewerb „Unser Dorf soll schöner werden" – ein Instrument zur Neuordnung des ländlichen Raumes. Erholung – ein wachsender Anspruch an eine sich wandelnde Landschaft.
1968. 196 S. ISBN 3-7843-2003-1

Heft 5: Landschaftsplan und Naturparke.
1970. 211 S. ISBN 3-7843-2005-8

Heft 6: Naturschutz und Erziehung; Landschaftsplanung – Bauleitplanung; Naturschutzgebiete und ihre Probleme. Seminare im Europäischen Naturschutzjahr 1970.
1971. 279 S. ISBN 3-7843-2006-6

Heft 7: Aktuelle Probleme des Schutzes von Pflanzen- und Tierarten.
1972. 143 S. ISBN 3-7843-2007-4

Heft 8: Internationale Arbeit in Naturschutz und Landschaftspflege.
Öffentlichkeitsarbeit für Naturschutz und Landschaftspflege.
1973. 178 S. ISBN 3-7843-2008-2

Heft 13: Untersuchungen zu Nationalparken in der Bundesrepublik Deutschland:
1. Henke, H.: Untersuchung der vorhandenen und potentiellen Nationalparke in der Bundesrepublik Deutschland im Hinblick auf das internationale Nationalparkkonzept.
2. Gutachtliche Stellungnahme der Bundesforschungsanstalt für Naturschutz und Landschaftsökologie zu einem umfassenden Naturschutz, insbesondere zur Einrichtung eines Nationalparks, im Nordfriesischen Wattenmeer.

1976. 180 S. ISBN 3-7843-2013-9

Heft 17: Zvolský, Z.: Erarbeitung von Empfehlungen für die Aufstellung von Landschaftsplanungen im Rahmen der allgemeinen Landeskultur und Agrarplanung.
1978. 262 S. ISBN 3-7843-2017-1

Heft 18: Blab, J.: Biologie, Ökologie und Schutz von Amphibien. 3., erweiterte und neubearbeitete Auflage.
1986. 150 S. ISBN 3-88949-128-6

Heft 21: Koeppel, H.-W. und Arnold, F.: Landschafts-Informationssystem.
1981. 192 S. ISBN 3-7843-2021-X

Heft 24: Blab, J.: Grundlagen des Biotopschutzes für Tiere. Ein Leitfaden zum praktischen Schutz der Lebensräume unserer Tiere. 4., erweiterte und neubearbeitete Auflage.
1993. 479 S. ISBN 3-88949-115-4

Heft 26: Bless, R.: Zur Regeneration von Bächen der Agrarlandschaft, eine ichthyologische Fallstudie,
1985. 80 S. ISBN 3-7843-2026-0

Heft 27: Mader, H.-J., Klüppel, R. und Overmeyer, H.: Experimente zum Biotopverbundsystem – tierökologische Untersuchungen an einer Anpflanzung.
1986. 136 S. ISBN 3-7843-2027-9

Heft 29: Blab, J. und Nowak, E. (Hrsg.): Zehn Jahre Rote Liste gefährdeter Tierarten in der Bundesrepublik Deutschland. Situation, Erhaltungszustand, neuere Entwicklungen.
1989. 312 S. ISBN 3-88949-157-X

Heft 30: Blab, J., Terhardt, A. und Zsivanovits, K.-P.: Tierwelt in der Zivilisationslandschaft. 1. Raumeinbindung und Biotopnutzung bei Säugetieren und Vögeln im Drachenfelser Ländchen.
1989. 223 S. ISBN 3-88949-158-8

Heft 31: Faber, T. F.: Die Luftbildauswertung, eine Methode zur ökologischen Analyse von Strukturveränderungen bei Fließgewässern.
1989. 119 S. ISBN 3-7843-2029-5

Heft 32: Riecken, U. (Hrsg.): Möglichkeiten und Grenzen der Bioindikation durch Tierarten und Tiergruppen im Rahmen raumrelevanter Planungen.
1990. 228 S. ISBN 3-7843-2071-6

Heft 33: Schulte, W. u.a.: Zur Biologie städtischer Böden. Beispielraum: Bonn-Bad Godesberg.
1990. 184 S. ISBN 3-88949-168-5

Heft 34: Blab, J., Brüggemann, P. und Sauer, H.: Tierwelt in der Zivilisationslandschaft. 2. Raumeinbindung und Biotopnutzung bei Reptilien und Amphibien im Drachenfelser Ländchen.
1991. 94 S. ISBN 3-88949-175-8

Heft 35: Bless, R.: Einsichten in die Ökologie der Elritze – *Phoxinus phoxinus (L.),* praktische Grundlagen zum Schutz einer gefährdeten Fischart.
1992. 57 S. ISBN 3-7843-2030-9

Heft 37: Gießübel, J.: Erfassung und Bewertung von Fließgewässern durch Luftbildauswertung.
1993. 77 S. ISBN 3-7843-2033-3

Heft 38: Blab, J. und Riecken, U.: Grundlagen und Probleme einer Roten Liste der gefährdeten Biotoptypen Deutschlands. Referate und Ergebnisse des gleichnamigen Symposiums der Bundesforschungsanstalt für Naturschutz und Landschaftsökologie vom 28.–30. Oktober 1991.
1993. 339 S. ISBN 3-88949-192-8

Heft 39: Haarmann, K. und Pretscher, P.: Zustand und Zukunft der Naturschutzgebiete in Deutschland – Die Situation im Süden und Ausblicke auf andere Landesteile.
1993. 266 S. ISBN 3-7843-2032-5

Heft 40: Blab, J., Schröder, E. und Völkl, W. (Hrsg.): Effizienzkontrollen im Naturschutz. Referate und Ergebnisse des gleichnamigen Symposiums vom 19.–21. Oktober 1992.
1994. 300 S. ISBN 3-88949-193-6

Heft 41: Riecken, U., Ries, U. und Ssymank, A.: Rote Liste der gefährdeten Biotoptypen der Bundesrepublik Deutschland.
1994. 184 S. ISBN 3-88949-194-4

Heft 42: Nowak, E., Blab, J. und Bless, R.: Rote Liste der gefährdeten Wirbeltiere in Deutschland.
1994. 190 S. ISBN 3-88949-195-2

Heft 43: Riecken, U. und Schröder, E. (Bearb.): Biologische Daten für die Planung. Auswertung, Aufbereitung und Flächenbewertung.
1995. 427 S. ISBN 3-7843-2078-5

Heft 44: Nordheim, H. von und Merck, T. (Bearb.): Rote Liste der Biotoptypen, Tier- und Pflanzenarten des deutschen Wattenmeer- und Nordseebereichs.
1995. 139 S. ISBN 3-89624-101-X

Heft 45: Arbeitsgemeinschaft Naturschutz der Landesämter, Landesanstalten und Landesumweltämter, Arbeitskreis CIR-Bildflug (Bearb.): Systematik der Biotoptypen- und Nutzungstypenkartierung (Kartieranleitung) (vergriffen) (Neuaufl. dt./engl. in Vorbereitung).
1995. 154 S. ISBN 3-89624-100-1

Heft 46: Boye, P., Kugelschafter, K., Meinig, H. und Pelz, H.-J. (Bearb.): Säugetiere in der Landschaftsplanung. Standardmethoden und Mindestanforderungen für säugetierkundliche Beiträge zu Umwelt- und Naturschutzplanungen.
1996. 186 S. ISBN 3-89624-102-8

Heft 48: Merck, T. und Nordheim, H. von (Bearb.): Rote Listen und Artenlisten der Tiere und Pflanzen des deutschen Meeres- und Küstenbereichs der Ostsee.
1996. 108 S. ISBN 3-89624-104-4

Heft 49: Klein, M. (Bearb.): Naturschutz und Erstaufforstung, Referate und Ergebnisse der gleichnamigen Fachtagung vom 6.-7. November 1995.
1997. 171 S. ISBN 3-89624-107-9

Heft 50/1: Finck, P., Haucke, U., Schröder, E., Forst, R. und Woithe, G.: Naturschutzfachliche Landschafts-Leitbilder. Rahmenvorstellungen für das Nordwestdeutsche Tiefland aus bundesweiter Sicht.
1997. 266 S. ISBN 3-89624-106-0

Heft 51: Mitlacher, G.: Ramsar-Bericht Deutschland.
1997. 190 S. ISBN 3-89624-108-7

Heft 52: Boedecker, D. und Nordheim, H. von (Bearb.): Naturschutz und Küstenschutz an der deutschen Ostseeküste. Ergebnisse einer Vilmer Expertentagung zum Erhalt der natürlichen Küstenmorphodynamik.
1997. 116 S. ISBN 3-89624-105-2

Heft 53: Ssymank, A., Haucke, U., Schröder, E., Rückriem, C. und Schröder, E., unter Mitarbeit von Messer, D.: Das europäische Schutzgebietssystem NATURA 2000: BfN-Handbuch zur Umsetzung der Fauna-Flora-Habitat-Richtlinie und der Vogelschutzrichtlinie.
2. Aufl. 2000. 565 S. ISBN 3-89624-113-3

Heft 54: Klein, M., Riecken, U. und Schröder, E. (Bearb.): Alternative Konzepte des Naturschutzes für extensiv genutzte Kulturlandschaften. Referate und Ergebnisse der gleichnamigen Fachtagung auf der Insel Vilm vom 10. – 12. Oktober 1996.
2. Aufl. 1999. 310 S. ISBN 3-89624-109-5

Heft 55: Bundesamt für Naturschutz (Hrsg.): Rote Liste gefährdeter Tiere Deutschlands.
1998. 434 S. ISBN 3-89624-110-9

Heft 56: Finck, P., Klein, M., Riecken, U. und Schröder, E. (Bearb.): Schutz und Förderung dynamischer Prozesse in der Landschaft. Referate und Ergebnisse der gleichnamigen Fachtagung auf der Insel Vilm vom 26.–28. August 1997.
1998. 424 S. ISBN 3-89624-111-7

Heft 57: Schopp-Guth, A.: Renaturierung von Moorlandschaften. Naturschutzfachliche Anforderungen aus bundesweiter Sicht unter besonderer Berücksichtigung der Grundwassermoore.
1999. 220 S. ISBN 3-89624-112-5

Heft 58: Dröschmeister, R. und Gruttke, H. (Bearb.): Die Bedeutung ökologischer Langzeitforschung für Naturschutz. Referate und Ergebnisse des gleichnamigen Symposiums auf der Insel Vilm vom 26.–30. Mai 1997.
1998. 436 S. ISBN 3-89624-114-1

Heft 59: Raths, U. und Riecken, U.: Laufkäfer (Col.: Carabidae) im Drachenfelser Ländchen. Raumeinbindung und Biotopnutzung sowie Aspekte zur Methodenoptimierung und Landschaftsentwicklung. Tierwelt in der Zivilisationslandschaft. Teil III.
1999. 156 S. ISBN 3-89624-115-X

Heft 60: Haupt, H., Lutz, K. und Boye, P. (Bearb.): Internationale Impulse für den Schutz von Wasservögeln in Deutschland. Ziele und Anforderungen des afrikanisch-eurasischen Wasservogelabkommens (AEWA) aus nationaler Sicht. Vorträge und Diskussionen zur Fachtagung des Bundesumweltministeriums und des Bundesamtes für Naturschutz „Konzepte und Maßnahmen zur Erhaltung gefährdeter Wasservogelarten in Mitteleuropa: Beiträge zur Aktionsplan des afrikanisch-eurasischen Wasservogelabkommens (AEWA)“ vom 22.–25. September 1998 in der Internationalen Naturschutzakademie Insel Vilm.
2000. 306 S. ISBN 3-7843-3602-7

Heft 61: Riecken, U.: Raumeinbindung und Habitatnutzung epigäischer Arthropoden unter den Bedingungen der Kulturlandschaft. Tierwelt in der Zivilisationslandschaft. Teil IV.
2000. 214 S. ISBN 3-7843-3600-0

Heft 62: Bischoff, C. and Dröschmeister, R. (eds): European Monitoring for Nature Conservation. Proceedings of the International Symposium 'Monitoring for Nature Conservation at a European Level', Isle of Vilm, Germany, 1–5 March 1999.
2000. 200 S. ISBN 3-7843-3601-9

Heft 63: Ssymank, A. (Bearb.): Vorrangflächen, Schutzgebietssysteme und naturschutzfachliche Bewertung großer Räume in Deutschland. Referate und Ergebnisse einer Fachtagung auf der Insel Vilm vom 19. bis 21. November 1998.
2000. 422 S. ISBN 3-7843-3603-5

Heft 64: Ssymank, A.: Vegetation und blütenbesuchende Insekten in der Kulturlandschaft. Pflanzengesellschaften, Blühphänologie, Biotopbindung und Raumnutzung von Schwebfliegen (Diptera, Syrphidae) im Drachenfelser Ländchen sowie Methodenoptimierung und Landschaftsbewertung.
2001. 514 S. ISBN 3-7843-3607-8

Heft 65: Binot-Hafke, M., Gruttke, H., Ludwig, G. und Riecken, U. (Bearb.): Bundesweite Rote Listen – Bilanzen, Konsequenzen, Perspektiven. Referate und Ergebnisse des gleichlautenden Fachsymposiums in Bonn vom 22.–23. März 1999.
2000. 255 S. ISBN 3-7843-3604-3

Heft 66: Meschede, A. und Heller, K.-G.: Ökologie und Schutz von Fledermäusen in Wäldern unter besonderer Berücksichtigung wandernder Arten.
2000. 374 S. ISBN 3-7843-3605-1

Heft 68: Petersen, B., Hauke, U. und Ssymank, A. (Bearb.): Der Schutz von Tier- und Pflanzenarten bei der Umsetzung der FFH-Richtlinie. Referate und Ergebnisse eines Workshops auf der Insel Vilm vom 22.–26. November 1999.
2000. 186 S. ISBN 3-7843-3606-X

Heft 72: Yousef, Mohamed A. M., Schubert, H. und Nordheim, H. von (Eds.): Charophytes in the Baltic Sea. Threats and Conservation.
2001. 44 S. ISBN 3-7843-3609-4

Schriftenreihe für Vegetationskunde

Heft 14: Krause, A. und Schröder, L.: Vegetationskarte der Bundesrepublik Deutschland 1 : 200 000 – Potentielle natürliche Vegetation – Blatt CC 3118 Hamburg-West. 2., unveränd. Aufl.
1994. 138 S. ISBN 3-7843-2064-3

Heft 15: Bohn, U.: Vegetationskarte der Bundesrepublik Deutschland 1 : 200 000 – Potentielle natürliche Vegetation – Blatt CC 5518 Fulda. 2., erw. Aufl.
1996. 364 S. ISBN 3-7843-2076-7

Heft 20: Krause, A.: Rasenansaaten und ihre Fortentwicklung an Autobahnen – Beobachtungen zwischen 1970 und 1988.
1989. 125 S. ISBN 3-7843-2069-4

Heft 22: Fink, Hans G. u.a.: Synopse der Roten Listen Gefäßpflanzen. Übersicht der Roten Listen und Florenlisten für Farn- und Blütenpflanzen der Bundesländer, der Bundesrepublik Deutschland (vor dem 3. Oktober 1990) sowie der ehemaligen DDR.
1992. 262 S. ISBN 3-7843-2075-9

Heft 23: Bundesforschungsanstalt für Naturschutz und Landschaftsökologie (Hrsg.): Rote Listen gefährdeter Pflanzen in der Bundesrepublik Deutschland. Referate und Ergebnisse eines Arbeitstreffens in der Internationalen Naturschutzakademie, Insel Vilm, vom 25.–28. 11. 1991.
1992. 245 S. ISBN 3-7843-2074-0

Heft 24: Hügin, G. und Henrichfreise, A.: Naturschutzbewertung der badischen Oberrheinaue – Vegetation und Wasserhaushalt des rheinnahen Waldes.
1992. 48 S. ISBN 3-7843-2072-4

Heft 25: Lohmeyer, W. und Sukopp, H.: Agriophyten in der Vegetation Mitteleuropas.
1992. 185 S. ISBN 3-7843-2073-2

Heft 26: Schneider, C., Sukopp, U. und Sukopp, H.: Biologisch-ökologische Grundlagen des Schutzes gefährdeter Segetalpflanzen.
1994. 356 S. ISBN 3-7843-2077-5

Heft 27: Kowarik, I., Starfinger, U. und Trepl, L. (Bearb.): Dynamik und Konstanz. Festschrift für Herbert Sukopp.
1995. 490 S. ISBN 3-89624-000-5

Heft 28: Bundesamt für Naturschutz (Hrsg.): Rote Liste gefährdeter Pflanzen Deutschlands.
1996. 744 S. ISBN 3-89624-001-3
Tabellenteil auch in Diskettenversion erhältlich

Heft 30: Korsch, H.: Chorologisch-ökologische Auswertungen der Daten der Floristischen Kartierung Deutschlands. Teil II des Abschlußberichtes des Projektes Datenbank Gefäßpflanzen.
1999. 200 S. ISBN 3-7843-3500-4

Heft 31: Scholz, P.: Katalog der Flechten und flechtenbewohnenden Pilze Deutschlands.
2000. 298 S. ISBN 3-7843-3501-2

Heft 32: Klingenstein, F. und Wingender, R. (Bearb.): Erfassung und Schutz der genetischen Vielfalt von Wildpflanzenpopulationen in Deutschland. Referate und Ergebnisse des gleichlautenden Expertengesprächs vom 19.–22. Oktober 1998 im Bundesamt für Naturschutz, Internationale Naturschutzakademie, Insel Vilm.
2000. 188 S. ISBN 3-7843-3502-0

Heft 33: Schulte, W. und Voggenreiter, V.: Florenkartierungen als Beitrag für den Naturschutz im Siedlungsbereich. Beispielraum Bonn-Bad Godesberg.
2000. 319 S. ISBN 3-7843-3503-9

Heft 34: Koperski, M., Sauer, M., Braun, W. und Gradstein, S. R.: Referenzliste der Moose Deutschlands. Dokumentation unterschiedlicher taxonomischer Auffassungen.
2000. 519 S. ISBN 3-7843-3504-7

Angewandte Landschaftsökologie

Heft 4: Bundesamt für Naturschutz (Hrsg.): Klimaänderungen und Naturschutz.
1995. 236 S. ISBN 3-89624-300-4

Heft 5: Schiller, J. und Könze, M. (Bearb.): Verzeichnis der Landschaftspläne und Landschaftsrahmenpläne in der Bundesrepublik Deutschland. Landschaftsplanverzeichnis 1993. 11. Fortschreibung. Gesamtausgabe.
1995. 426 S. ISBN 3-89624-301-2

Heft 6: Thomas, A., Mrotzek, R. und Schmidt, W.: Biomonitoring in naturnahen Buchenwäldern.
1995. 140 S. ISBN 3-89624-302-4

Heft 7: Institut für Bahntechnik GmbH, Berlin: Auswirkungen eines neuen Bahnsystems auf Natur und Landschaft. Untersuchungen zur Bauphase der Magnetschwebebahn Transrapid.
1996. 226 S. ISBN 3-89624-305-5

Heft 8: Krause, C. L. und Klöppel, D.: Landschaftsbild in der Eingriffsregelung. Hinweise zur Berücksichtigung von Landschaftsbildelementen.
1996. 196 S. ISBN 3-89624-303-9

Heft 9: Ad-hoc-AG Geotopschutz/Ad-hoc Geotope Conservation Working Group: Arbeitsanleitung Geotopschutz in Deutschland. Geotope Conservation in Germany. (dt./engl.)
1996. 114 S. ISBN 3-89624-306-3

Heft 11: Oppermann, B., Luz, F. und Kaule, G.: Der „Runde Tisch" als Mittel zur Umsetzung der Landschaftsplanung. Chancen und Grenzen der Anwendung eines kooperativen Planungsmodells mit der Landwirtschaft.
1997. 104 S. ISBN 3-89624-308-X

Heft 12: Borggräfe, K. und Kölsch, O.: Naturschutz in der Kulturlandschaft: Das Erprobungs- und Entwicklungsvorhaben „Revitalisierung in der Ise-Niederung".
1997. 122 S. ISBN 3-89624-309-8

Heft 13: Arens, R. und Neff, R.: Versuche zur Erhaltung von Extensivgrünland. Aus dem wissenschaftlichen Begleitprogramm zum E+E-Vorhaben des BfN „Renaturierung des NSG Rotes Meer/Hohe Rhön"
1997. 176 S. ISBN 3-89624-311-X

Heft 14: Forst, M., Hierlmeier, R., Kiebel, A. und Ruthsatz, B.: Hoch- und Zwischenmoore in Trockenmaaren der Vulkaneifel.
1997. 482 S. ISBN 3-89624-310-1

Heft 15: Rosenthal, G. u.a.: Feuchtgrünland in Norddeutschland. Ökologie, Zustand, Schutzkonzepte.
1998. Textband: 318 S., Kartenband: 31 Karten + 2 Abb.
(Text- und Kartenband nur gemeinsam erhältlich) ISBN 3-89624-314-4

Heft 16: Wollny-Goerke, K.: Das Informations- und Umweltbildungskonzept der Seehundstation Friedrichskoog.
1998. 122 S. ISBN 3-89624-312-8

Heft 17: Gruehn, D. und Kenneweg, H.: Berücksichtigung der Belange von Naturschutz und Landschaftspflege in der Flächennutzungsplanung.
1998. 492 S. ISBN 3-89624-313-6

Heft 18: Hagius, A. und Scherfose, V. (Bearb.): Pflege- und Entwicklungsplanung in Naturschutzgroßprojekten des Bundes.
1999. 188 S. ISBN 3-89624-316-0

Heft 19: Schemel, H.-J. u. a.: Naturerfahrungsräume. Ein humanökologischer Ansatz für naturnahe Erholung in Stadt und Land.
1998. 374 S. ISBN 3-89624-315-2

Heft 20: Burggraaff, P. und Kleefeld, K.-D.: Historische Kulturlandschaft und Kulturlandschaftselemente.
1998. 320 S. ISBN 3-89624-318-7

Heft 21: Reck, H. u. a.: Die Entwicklung neuer Lebensräume auf landwirtschaftlich genutzten Flächen.
1999. 146 S. ISBN 3-89624-321-7

Heft 22: Rückriem, C. und Roscher, S.: Empfehlungen zur Umsetzung der Berichtspflicht gemäß Artikel 17 der Fauna-Flora-Habitat-Richtlinie.
1999. 456 S. ISBN 3-89624-322-5

Heft 23: Bundesamt für Naturschutz (Hrsg.): Fortschritte für Naturschutz und Landschaftspflege an Wasserläufen.
1998. 206 S. ISBN 3-89624-317-9

Heft 24: Schweppe-Kraft, B.: Monetäre Bewertung von Biotopen und ihre Anwendung bei Eingriffen in Natur und Landschaft. (Dissertat./TU Berlin).
1998. 314 S. ISBN 3-89624-319-5

Heft 25: Degenhardt, S. u. a.: Zahlungsbereitschaft für Naturschutzprogramme.
1998. 200 S. ISBN 3-89624-320-9

Heft 26: Planungsgruppe Ökologie und Umwelt & W. Erbguth: Möglichkeiten der Umsetzung der Eingriffsregelung in der Bauleitplanung. Zusammenwirken von Landschaftsplanung, naturschutzrechtlicher Eingriffsregelung und Bauleitplanung.
1999. 238 S. ISBN 3-89624-323-3

Heft 27: Abresch, J.-P., Gassner, E. und Korff, J. v.: Naturschutz und Braunkohlesanierung.
2000. 428 S. ISBN 3-7843-3702-3

Heft 28: Bosch & Partner GmbH und ARSU GmbH: Beurteilungskriterien für die Auswirkungen des Bundeswasserstraßenausbaus auf Natur und Landschaft.
1999. 80 S. ISBN 3-7843-3700-7

Heft 29: Bundesamt für Naturschutz (Hrsg.): Weiterentwicklung der Landschaftsrahmenplanung und ihre Integration in die Regionalplanung.
2000. Textband 314 S., Begleitbroschüre 74 S.
(Text- und Begleitbroschüre nur gemeinsam erhältlich) ISBN 3-7843-3701-5

Heft 30: Bornholdt, G., Braun, H. und Kress, J. C.: Erfolgskontrollen im abgeschlossenen Naturschutzgroßprojekt „Hohe Rhön/Lange Rhön".
2000. 262 S. ISBN 3-7843-3704-X

Heft 31: Bosch & Partner GmbH und Wolf, R.: Wiederherstellungsmöglichkeiten von Bodenfunktionen im Rahmen der Eingriffsregelung.
2000. 170 S. + Anhang ISBN 3-7843-3708-2

Heft 32: Pfadenhauer, J. u. a.: Sicherung und Entwicklung der Heiden im Norden von München.
2000. 312 S. ISBN 3-7843-3703-1

Heft 33: Statistisches Bundesamt und Bundesamt für Naturschutz (Hrsg.): Konzepte und Methoden zur Ökologischen Flächenstichprobe – Ebene II: Monitoring von Pflanzen und Tieren.
2000. 262 S. und 1 Falttafel ISBN 3-7843-3705-8

Heft 34: Schweppe-Kraft, B. (Bearb.): Innovativer Naturschutz – Partizipative und marktwirtschaftliche Instrumente. Referate und Ergebnisse der Tagung „Innovative Instrumente des Naturschutzes – Konsequenzen für Forschung, Politik und Praxis" vom 1.–4. Dezember 1997 im Bundesamt für Naturschutz, Internationale Naturschutzakademie, Insel Vilm.
2000. 226 S. ISBN 3-7843-3706-6

Heft 36: Borggräfe, K., Kölsch, O. und Lucker, T.: Entwicklungspotenziale der Natur in der Kulturlandschaft. Wissenschaftliche Ergebnisse aus der Modellregion Ise-Niederung. Abschlussbericht zur wissenschaftlichen Begleitung des E+E-Vorhabens „Revitalisierung der Ise-Niederung".
2001. 216 S. ISBN 3-7843-3709-0

Heft 37: Bundesamt für Naturschutz (Hrsg.): Renaturierung von Bächen, Flüssen und Strömen. Tagungsband zur gleichnamigen internationalen Fachtagung vom 24.–26. November 1999 in Neuhaus im Solling.
2001. 340 S. ISBN 3-7843-3710-4

Heft 38: Nick, K.-J., Löpmeier, F.-J., Schiff, H. u.a.: Moorregeneration im Leegmoor/Emsland nach Schwarztorfabbau und Wiedervernässung. Ergebnisse aus dem E+E-Vorhaben 809 01 001 des Bundesamtes für Naturschutz.
2001. 204 S. ISBN 3-7843-3713-9

Heft 39: Bornholdt, G., Hamm, S., Kress, J.C., Brenner, U. und Malten, A.: Zoologische Untersuchungen zur Grünlandpflege am Beispiel von Borstgrasrasen und Goldhaferwiesen in der Hohen Rhön. Ergebnisse aus dem F+E-Vorhaben 808 04 004 des Bundesamtes für Naturschutz.
2001. 238 S. ISBN 3-7843-3711-2

Heft 40: Voigtländer, U., Scheller, W. und Martin, C.: Ursachen für die Unterschiede im biologischen Inventar der Agrarlandschaft in Ost- und Westdeutschland.
2001. 408 S. ISBN 3-7843-3714-7

Heft 41: Knickel, K.-H., Janßen, B., Schramek, J. und Käppel, K.: Naturschutz und Landwirtschaft: Kriterienkatalog zur „Guten fachlichen Praxis". Ergebnisse aus dem F+E-Vorhaben 898 88 032 des Bundesamtes für Naturschutz.
2001. 152 S. ISBN 3-7843-3712-0

Sonstige Veröffentlichungen

Landschaftsbild – Eingriff – Ausgleich. Handhabung der naturschutzrechtlichen Eingriffsregelung für den Bereich Landschaftsbild.
1991. 244 S. ISBN 3-7843-2511-4

Landschaftsplanung als Entwicklungschance für umweltverträgliche Flächennutzungsplanung. Landschaftsplanung, Bauleitplanung, Umweltplanung, Verkehrsprojekte in Ost und West.
1994. 257 S. ISBN 3-7843-2681-1

Lange, D.: Untersuchungen zum Heilpflanzenhandel in Deutschland. Ein Beitrag zum internationalen Artenschutz.
1996. 146 S. + Anhang ISBN 3-89624-604-6

Lange, D. and Schippmann, U.: Trade Survey of Medicinal Plants in Germany. A Contribution to International Plant Species Conservation.
1997. 146 S. + Anhang ISBN 3-89624-607-0

Kasparek, M., Gröger, A. and Schippmann, U.: Directory for Medicinal Plants Conservation. Networks, Organizations, Projects, Information Sources.
1996. 156 S. ISBN 3-89624-606-2

Bundesamt für Naturschutz (Hrsg.): Erhaltung der biologischen Vielfalt. Wissenschaftliche Analyse deutscher Beiträge.
1997. 352 S. ISBN 3-89624-610-0

Koptyug, V. A. and Uppenbrink, M. (Eds.): Sustainable Development of the Lake Baikal Region. A Model Territory for the World. (Nato ASI Series. Partnership Sub-Series 2: Environment, 6)
Springer Verlag 1996. 372 S. ISBN 3-540-60560-6

Bundesamt für Naturschutz (Hrsg.): Biodiversität und Tourismus. Konflikte und Lösungsansätze an den Küsten der Weltmeere.
Springer Verlag 1997. 339 S. ISBN 3-540-62393-0
englische Ausgabe: Biodiversity and Tourism. ISBN 3-540-62395-7

Cunningham, M., Cunningham, A. B. and Schippmann, U.: Trade in Prunus africana and the Implementation of CITES.
1997. 52 S. ISBN 3-89624-608-9

Carter, S. and Eggli, U.: The CITES Checklist of Succulent Euphorbia Taxa (Euphorbiaceae).
1997. 90 S. ISBN 3-89624-609-7

Steinmetz, M., Pütsch, M. und Bisschopinck, T.: Untersuchungen zur Transportmortalität beim Import von Vögeln und Reptilien nach Deutschland. Mit einer Studie zu den Prä-Export-Bedingungen in Tansania.
1998. 130 S. ISBN 3-89624-611-9

Steinmetz, M., Pütsch, M. and Bisschopinck, T.: Transport Mortality during the Import of Wild Caught Birds and Reptiles to Germany. (Including a Study on Pre-Export-Conditions in the United Republic of Tanzania).
1998. ISBN 3-89624-613-5

Jelden, D., Sprotte, I. und Gruschwitz, M. (Bearb.): Nachhaltige Nutzung. Referate und Ergebnisse des gemeinsamen Symposiums des Bundesamtes für Naturschutz (BfN) und des Bundesverbandes für fachgerechten Natur- und Artenschutz (BNA) in der Internationalen Naturschutzakademie Insel Vilm vom 22.–24. Oktober 1997.
1998. 142 S. ISBN 3-89624-612-7

Bundesamt für Naturschutz (Hrsg.): Fledermäuse und Fledermausschutz in Deutschland/Bats and Bat Conservation in Germany (dt./engl.).
1999. 110 S. ISBN 3-89624-614-3

Bundesamt für Naturschutz (Hrsg.): Botanische Gärten und Biodiversität. Erhaltung Biologischer Vielfalt durch Botanische Gärten und die Rolle des Übereinkommens über die Biologische Vielfalt (Rio de Janeiro, 1992).
1999. 84 S. ISBN 3-89624-615-1

Federal Agency for Nature Conservation (ed.): Botanic Gardens and Biodiversity.
2000. 82 S. ISBN 3-7843-3810-0

Brendle, U.: Musterlösungen im Naturschutz – Politische Bausteine für erfolgreiches Handeln.
1999. 262 S. ISBN 3-7843-3800-3

Bundesamt für Naturschutz (Hrsg.): Daten zur Natur 1999.
1999. 266 S. ISBN 3-7843-3801-1

Federal Agency for Nature Conservation (ed.): Nature Data 1999.
2000. 266 S. ISBN 3-7843-3807-0

Bennert, H. W.: Die seltenen und gefährdeten Farnpflanzen Deutschlands.
1999. 382 S. ISBN 3-7843-3802-x

Bundesamt für Naturschutz (Hrsg.): Naturschutzbilanzen.
1999. 158 S. ISBN 3-7843-3803-8

Mäck, U. und Jürgens, M.-E.: Aaskrähe, Elster und Eichelhäher in Deutschland.
1999. 252 S. ISBN 3-7843-3804-6

Andrian-Werburg, F. von, Jordan, R., Küttner, A., Niemann, N. B., Schiller, J., Tobias, K. und Winkelbrandt, A. (Bearb.): Planzeichen für die örtliche Landschaftsplanung.
2000. 26 S. ISBN 3-7843-3805-4

Rauer, G., Driesch, M. von den, Ibisch, P. L., Lobin, W. und Barthlott, W.: Beitrag der deutschen Botanischen Gärten zur Erhaltung der Biologischen Vielfalt und Genetischer Ressourcen. Bestandsaufnahme und Entwicklungskonzept.
2000. 246 S. ISBN 3-7843-3806-2

Lange, D.: Conservation and Sustainable Use of *Adonis vernalis*, a Medicinal Plant in International Trade. Plant Species Conservation Monographs 1.
2000. 88 S. ISBN 3-7843-3811-9

Bundesamt für Naturschutz (Hrsg.): Empfehlungen des Bundesamtes für Naturschutz zu naturschutzverträglichen Windkraftanlagen.
2000. 224 S. ISBN 3-7843-3813-5

Korn, H. und Feit, U. (Bearb.): Treffpunkt Biologische Vielfalt. Interdisziplinärer Forschungsaustausch im Rahmen des Übereinkommens über die biologische Vielfalt.
2001. 247 S.
ISBN 3-7843-3815-1

Driesch, M. von den und Lobin, W. (Bearb.): Botanische Gärten und Erhaltung Biologischer Vielfalt. Ein Erfahrungsaustausch. (dt./russ.)
2001. 154 S.
ISBN 3-7843-3813-5

Wolfrum, R., Klepper, G., Stoll, P.-T. und Franck, S.: Genetische Ressourcen, traditionelles Wissen und geistiges Eigentum im Rahmen des Übereinkommens über die biologische Vielfalt.
2001. 202 S.
ISBN 3-7843-3817-8

Gruehn, D. (Bearb.): Landschaftsplanung und ihre Wechselwirkungen zu anderen Fachplanungen. Dokumentation der Fachtagung am 15. und 16. Juni 2000 aus Anlass des fünfjährigen Bestehens der BfN-Außenstelle am Dienstort Leipzig.
2001. 178 S.
ISBN 3-7843-3821-6

Riede, K. (ed.): New Perspectives for Monitoring Migratory Animals – Improving Knowledge for Conservation.
2001. 164 S.
ISBN 3-7843-3819-4

Dinter, Wolfgang P.: Biogeography of the OSPAR Maritime Area. A Synopsis and Synthesis of Biogeographical Distribution Patterns described for the North-East Atlantic.
2001. 168 S.
ISBN 3-7843-3818-6

Gerstner, S., Jansen, St. und Lübbert, C.: Nachhaltige Erholungsnutzung und Tourismus in Bergbaufolgelandschaften. Handreichung für Kommunen.
2001. 162 S.
ISBN 3-7843-3823-2

Erdmann, K.-H. und Schell, C. (Bearb.): Naturschutz und gesellschaftliches Handeln. Aktuelle Beiträge aus Wissenschaft und Praxis.
2002. 248 S.
ISBN 3-7843-3822-4

Auslieferung Schriftenreihen:
BfN-Schriftenvertrieb im Landwirtschaftsverlag GmbH
48084 Münster · Telefon 0 25 01 / 8 01-3 00 · Telefax 0 25 01 / 8 01-3 51

Natur und Landschaft, Zeitschrift für Naturschutz, Landschaftspflege und Umweltschutz
Verlag: Kohlhammer GmbH, 70549 Stuttgart, Tel. 07 11/78 63-3 03, Fax: 07 11/78 63-4 30.
Erscheinungsweise: monatlich.
Bestellungen nimmt der Verlag entgegen und übersendet auf Anforderung Probehefte.

Dokumentation Natur und Landschaft-online.
Die Literaturdatenbank für Naturschutz und Landschaftspflege im Internet.
Kostenloser Zugriff unter: www.bfn.de; Recherche/zentrale Literaturdatenbank

Bibliographien Sonderhefte der Dokumentation Natur und Landschaft
Erscheinungsweise: unregelmäßig

Nr.		Anzahl der Titel
So.-H. 22: (1995)	Arktische Gebiete. Eine Literaturdokumentation zur Umweltsituation des russischen Arktis-Anteils (= Bibliographie Nr. 68)	213
So.-H. 23: (1995)	Streuobst. Bindeglied zwischen Naturschutz und Landwirtschaft (= Bibliographie Nr. 69)	1544
So.-H. 24: (1995)	Naturschutzgebiet Lüneburger Heide. (= Bibliographie Nr. 70)	1077
So.-H. 25: (1995)	Naturschutz und Landschaftspflege im besiedelten Bereich. Literaturnachträge 1992 bis 1995. (= Bibliographie Nr. 71)	908
So.-H. 26: (1997)	Biosphärenreservate (= Bibliographie Nr. 72)	938
So.-H. 27: (1997)	Naturschutz und Windkraft (= Bibliographie Nr. 74)	240
	Lärmwirkungen auf Tiere (= Bibliographie Nr. 75)	618
So.-H. 28: (1997)	Das Wattenmeer - Ein gefährdeter Lebensraum (= Bibliographie Nr. 76)	2686
So.-H. 29: (1997)	Insekten im Naturhaushalt (= Bibliographie Nr. 77)	1854
So.-H. 30: (1999)	Naturschutzgebiete und Großschutzgebiete im Land Sachsen-Anhalt (= Bibliographie Nr. 79)	2577
	Bibliographie zur Herpetofauna des Landes Sachsen-Anhalt. 2. Fassung (= Bibliographie Nr. 80)	490
So.-H. 31: (2000)	Naturschutz und Landschaftspflege im besiedelten Bereich. Literaturnachträge bis 1999. (= Bibliographie Nr. 81)	1076

Vertrieb: Verlag Kohlhammer GmbH
70549 Stuttgart, Tel.: 07 11/78 63-3 03, Fax: 07 11/78 63-4 30.

MAB-Mitteilungen

28. Lieth, H. et al.: Problems with future land-use changes in rural areas. Working meeting for the organization of an UNESCO theme study November 2–5, 1987, in Osnabrück. September 1988

29. Lewis, R.A.; Paulus, M.; Horras, C. und Klein, B.: Auswahl und Empfehlung von Ökologischen Umweltbeobachtungsgebieten in der Bundesrepublik Deutschland. Mai 1989

30. Weigmann, G. (Hrsg.): Report on MAB-Workshop „International scientific workshop on soils and soil zoology in urban ecosystems as a basis for management and use of green open spaces" in Berlin, September 15–19, 1986. Oktober 1989

32. Brettschneider, G.: Vermittlung ökologischen Wissens im Rahmen des MAB-Programms. Erarbeitung eines spezifischen Programmbeitrages für das UNESCO-Programm „Man and the Biosphere" (MAB). April 1990

33. Goerke, W.; Nauber, J. und Erdmann, K.-H. (Hrsg.): Tagung der MAB-Nationalkomitees der Bundesrepublik Deutschland und der Deutschen Demokratischen Republik am 28. und 29. Mai 1990 in Bonn. September 1990

34. Ashdown, M. und Schaller, J.: Geographische Informationssysteme und ihre Anwendung in MAB-Projekten, Ökosystemforschung und Umweltbeobachtung / Geographic Information Systems and their Application in MAB Projects, Ecosystem Research and Environmental Monitoring. November 1990; 2. Auflage 1993

35. Kerner, H.F.; Spandau, L. und Köppel, J.G.: Methoden zur angewandten Ökosystemforschung – Werkstattbericht – MAB-6-Projekt „Ökosystemforschung Berchtesgaden", Band 1 und 2. September 1991

36. Erdmann, K.-H. und Nauber, J. (Hrsg.): Beiträge zur Ökosystemforschung und Umwelterziehung. 1992

37. Erdmann, K.-H. und Nauber, J. (Hrsg.): Beiträge zur Ökosystemforschung und Umwelterziehung II. 1993

38. Erdmann, K.-H. und Nauber, J. (Hrsg.): Beiträge zur Ökosystemforschung und Umwelterziehung III. 1996

39. Deutsches MAB-Nationalkomitee (Hrsg.): Entwicklungskonzept Bayerischer Wald, Sumava (Böhmerwald), Mühlviertel. 1994

40. German MAB National Committee (Ed.): Development concept Bavarian Forest, Sumava (Bohemian Forest), Mühlviertel. 1994

41. Kruse-Graumann, L. in cooperation with v. Dewitz, F.; Nauber, J. and Trimpin, A. (Eds.): Proceedings of the EUROMAB Workshop, 23 - 25 January 1995, Königswinter „Societal Dimensions of Biosphere Reserves - Biosphere Reserves for People." 1995

42. Kruse-Graumann, L.; Hartmuth, G. und Erdmann, K.-H. (Hrsg.) Ziele, Möglichkeiten und Probleme eines gesellschaftlichen Monitorings. 1998

43. Erdmann, K.-H.: Untersuchungen zur Bodenerosion im südlichen Nordrhein-Westfalen. 1998

44. Krieger, C.: Der Nationalpark Vorpommersche Boddenlandschaft und seine gesellschaftliche Akzeptanz. 1998

45. Erdmann, K.-H.; Bork, H.-R. und Grunewald, K. (Hrsg.): Geographie und Naturschutz. Beiträge zu einer naturverträglichen Entwicklung. 1998

Sonderausgaben des Deutschen Nationalkomitees für das UNESCO-Programm MAB

Goodland, R.; Daly, H.; El Serafy, S. und von Droste, B. (Hrsg.): Nach dem Brundtland-Bericht: Umweltverträgliche wirtschaftliche Entwicklung.
1992

Erdmann, K.-H. und Nauber, J.: Der deutsche Beitrag zum UNESCO-Programm „Der Mensch und die Biosphäre" (MAB) im Zeitraum Juli 1990 bis Juni 1992.
1993

Solbrig, O. T.: Biodiversität. Wissenschaftliche Fragen und Vorschläge für die internationale Forschung.
1994

Erdmann, K.-H. und Nauber, J.: Der deutsche Beitrag zum UNESCO-Programm „Der Mensch und die Biosphäre" (MAB) im Zeitraum Juli 1992 bis Juni 1994.
1995

Standing Working Group of the Biosphere Reserves in Germany (Ed.): Guidelines for protection, maintenance and development of the biosphere reserves in Germany.
1995

UNESCO (Hrsg.): Biosphärenreservate. Die Sevilla-Strategie und die Internationalen Leitlinien für das Weltnetz.
1996

Deutsches Nationalkomitee für das UNESCO-Programm „Der Mensch und die Biosphäre" (MAB) (Hrsg.): Kriterien für Anerkennung und Überprüfung von Biosphärenreservaten der UNESCO in Deutschland
1996

German National Committee for the UNESCO Programme „Man and the Biosphere" (MAB) (Ed.): Criteria for designation and evaluation of UNESCO biosphere reserves in Germany
1996

Die MAB-Veröffentlichungen sind zu beziehen über die MAB-Geschäftsstelle:
Bundesamt für Naturschutz, FG Internationales/MAB, Konstantinstr. 110, D-53179 Bonn
Tel.: 02 28 / 84 91-0, Fax: 02 28 / 84 91-2 00

Veröffentlichungen im Rahmen des MAB-Programms

Erdmann, K.-H. (Hrsg.): Perspektiven menschlichen Handelns: Umwelt und Ethik.
Springer-Verlag, Berlin-Heidelberg 1992 (2. Auflage 1993)

Erdmann, K.-H. und Kastenholz, H.G. (Hrsg.): Umwelt- und Naturschutz am Ende des 20. Jahrhunderts. Probleme, Aufgaben und Lösungen.
Springer-Verlag, Berlin-Heidelberg 1995

Ständige Arbeitsgruppe der Biosphärenreservate in Deutschland (Hrsg.): Biosphärenreservate in Deutschland. Leitlinien für Schutz, Pflege und Entwicklung.
Springer-Verlag, Berlin-Heidelberg 1995

Kastenholz, H.G.; Erdmann, K.-H. und Wolff, M. (Hrsg.): Nachhaltige Entwicklung. Zukunftschancen für Mensch und Umwelt.
Springer-Verlag, Berlin-Heidelberg 1996

Erdmann, K.-H. (Hrsg.): Internationaler Naturschutz.
Springer-Verlag, Berlin-Heidelberg 1997

Erdmann, K.-H. und Spandau, L. (Hrsg.): Naturschutz in Deutschland.
Eugen Ulmer Verlag, Stuttgart 1997

zu beziehen über den Buchhandel

Preisliste

Aus postalischen Gründen werden die Preise der Veröffentlichungen gesondert aufgeführt.

Im Landwirtschaftsverlag sind erschienen:

Schriftenreihe für Landschaftspflege und Naturschutz

Heft 1 = € 8,–
Heft 2 = € 5,–
Heft 3 = € 8,–
Heft 5 = € 5,–
Heft 6 = € 5,–
Heft 7 = € 5,–
Heft 8 = € 5,–
Heft 13 = € 12,–
Heft 17 = € 16,–
Heft 18 = € 16,–
Heft 21 = € 12,–
Heft 24 = € 35,–
Heft 26 = € 8,–
Heft 27 = € 8,–
Heft 29 = € 20,–
Heft 30 = € 16,–
Heft 31 = € 8,–
Heft 32 = € 16,–
Heft 33 = € 16,–
Heft 34 = € 12,–
Heft 35 = € 8,–
Heft 37 = € 14,–
Heft 38 = € 16,–
Heft 39 = € 16,–
Heft 40 = € 16,–
Heft 41 = € 16,–
Heft 42 = € 16,–
Heft 43 = € 20,–
Heft 44 = € 16,–
Heft 45 = € 16,–
Heft 46 = € 16,–
Heft 48 = € 12,–
Heft 49 = € 16,–
Heft 50/1 = € 20,–
Heft 51 = € 16,–
Heft 52 = € 12,–
Heft 53 = € 30,–
Heft 54 = € 20,–
Heft 55 = € 20,–
Heft 56 = € 20,–
Heft 57 = € 20,–
Heft 58 = € 20,–
Heft 59 = € 16,–
Heft 60 = € 20,–
Heft 61 = € 20,–
Heft 62 = € 20,–
Heft 63 = € 20,–
Heft 64 = € 20,–
Heft 65 = € 20,–
Heft 66 = € 20,–
Heft 68 = € 16
Heft 72 = € 12,–

Schriftenreihe für Vegetationskunde:

Heft 14 = € 14,–
Heft 15 = € 20,–
Heft 20 = € 14,–
Heft 22 = € 16,–
Heft 23 = € 16,–
Heft 24 = € 5,–
Heft 25 = € 14,–
Heft 26 = € 25,–
Heft 27 = € 25,–
Heft 28
(Buch) = € 20,–
(Diskette) = € 25,–
(Buch+Diskette) = € 35,–
Heft 30 = € 16,–
Heft 31 = € 16,–
Heft 32 = € 16,–
Heft 33 = € 16,–
Heft 34 = € 16,–

Angewandte Landschaftsökologie

Heft 4 = € 12,–
Heft 5 = € 12,–
Heft 6 = € 12,–
Heft 7 = € 12,–
Heft 8 = € 12,–
Heft 9 = € 12,–
Heft 11 = € 12,–
Heft 12 = € 12,–
Heft 13 = € 16,–
Heft 14 = € 20,–
Heft 15 = € 25,–
Heft 16 = € 12,–
Heft 17 = € 20,–
Heft 18 = € 12,–
Heft 19 = € 16,–
Heft 20 = € 16,–
Heft 21 = € 12,–
Heft 22 = € 20,–
Heft 23 = € 12,–
Heft 24 = € 16,–
Heft 25 = € 12,–
Heft 26 = € 12,–
Heft 27 = € 20,–
Heft 28 = € 12,–
Heft 29 = € 20,–
Heft 30 = € 16,–
Heft 31 = € 12,–
Heft 32 = € 16,–
Heft 33 = € 16,–
Heft 34 = € 12,–
Heft 36 = € 16,–
Heft 37 = € 16,–
Heft 38 = € 16,–
Heft 39 = € 16,–
Heft 40 = € 20,–
Heft 41 = € 14,–

Sonstige Veröffentlichungen:

Landschaftsbild – Eingriff – Ausgleich	€ 20,–
Landschaftsplanung als Entwicklungschance für umweltverträgliche Flächennutzungsplanung	€ 16,–
Directory for Medicinal Plants Conservation	€ 12,–
Untersuchungen zum Heilpflanzenhandel in Deutschland	€ 12,–
Trade Survey of Medicinal Plants in Germany	€ 12,–
Sustainable Development of the Lake Baikal Region	€ 125,–
Biodiversität und Tourismus. Konflikte und Lösungsansätze an den Küsten der Weltmeere	€ 50,–
Biodiversity and Tourism	€ 50,–
Trade in Prunus Africana and the Implementation of CITES	€ 12,–
The CITES Checklist of Succulent Euphorbia Taxa	€ 12,–
Erhaltung der biologischen Vielfalt	€ 20,–
Untersuchungen zur Transportmortalität	€ 12,–
Nachhaltige Nutzung	€ 12,–
Transport Mortality	€ 12,–
Fledermäuse und Fledermausschutz in Deutschland/ Bats and Bat Conservation in Germany	€ 12,–
Botanische Gärten und Biodiversität	€ 12,–
Botanic Gardens and Biodiversity	€ 12,–
Musterlösungen im Naturschutz	€ 16,–
Daten zur Natur 1999	€ 12,–
Nature Data 1999	€ 12,–
Die seltenen und gefährdeten Farnpflanzen Deutschlands	€ 40,–
Naturschutzbilanzen	€ 12,–
Aaskrähe, Elster und Eichelhäher in Deutschland	€ 12,–
Planzeichen für die örtliche Landschaftsplanung	€ 12,–
Beitrag der deutschen Botanischen Gärten zur Erhaltung der Biologischen Vielfalt und genetischer Ressourcen	€ 12,–
Conservation and Sustainable Use of *Adonis vernalis*	€ 12,–
Empfehlung des Bundesamtes für Naturschutz zu naturschutzverträglichen Windkraftanlagen	€ 16,–
Treffpunkt Biologische Vielfalt	€ 12,–
Botanische Gärten und Erhaltung Biologischer Vielfalt	€ 12,–
Genetische Ressourcen, traditionelles Wissen und geistiges Eigentum im Rahmen des Übereinkommens über die biologische Vielfalt	€ 12,–
Landschaftsplanung und ihre Wechselwirkungen zu anderen Fachplanungen	€ 12,–
New Perspectives for Monitoring Migratory Animals	€ 12,–
Biogeography of the OSPAR Maritime Area	€ 12,–
Nachhaltige Erholungsnutzung und Tourismus in Bergbaufolgelandschaften	€ 12,–
Naturschutz und gesellschaftliches Handeln	€ 14,–

Im Kohlhammer Verlag erscheinen:

Natur und Landschaft

Bezugspreis: € 60,90 jährlich (zzgl. Versandkosten € 5,20). Für Studenten € 40,80.
Einzelheft: € 6,40 (zzgl. Versandkosten).

Bibliographien, Sonderhefte der Dokumentation Natur und Landschaft:

So.-Heft 22 = € 8,–	So.-Heft 27 = € 12,–
So.-Heft 23 = € 16,–	So.-Heft 28 = € 20,–
So.-Heft 24 = € 12,–	So.-Heft 29 = € 16,–
So.-Heft 25 = € 12,–	So.-Heft 30 = € 16,–
So.-Heft 26 = € 14,–	So.-Heft 31 = € 12,–

The ministerial meeting of the „OSPAR Convention for the Protection of the Marine Environment of the North-East Atlantic" adopted a new Annex V to the OSPAR Convention in 1998.

Besides programmes of the OSPAR Convention for the prevention from pollution with hazardous and dangerous substances and the input of nutrients this new Annex V together with the Appendix 3 *inter alia* aims for the establishment of a representative system of Marine Protected Areas (MPAs) within the OSPAR maritime area.

The German Federal Agency for Nature Conservation conducted this study to identify biogeographical units of the North-East Atlantic and Arctic Oceans with relevance for the OSPAR maritime area to distinguish biogeographically representative areas for use within the OSPAR MPA-process. Such measures are particularly pressing according to the present situation of loss and change of marine biodiversity, and according to the related urgent call by the OSPAR Convention for action to protect, conserve and restore marine biological diversity against increasing anthropogenic threats.

Together with a broad presentation of oceanographical features which are the basis for marine biogeographic patterns, a selection of different biogeographic approaches to marine biogeography is presented in this work. A resulting synoptical new biogeographic concept which is a mainly watermass related ecosystem approach integrates the complex biogeographical distribution patterns of the pelagos and benthos in oceanic, neritic, and deep-sea spaces. This study might also serve as a compendium for marine biogeography of the North-East Atlantic.

ISBN 3-7843-3818-6